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REPORT # 4

THE EFFECT OF ENVIRONMENTAL PERTURBATIONS ON BENTHIC
COMMUNITIES: AN EXPERIMENT IN BENTHIC RECOLONIZATION
AND SUCCESSION IN LONG ISLAND SOUND

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This is presented to the Department of Geology and Geophysics,
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May 1973

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The project described here was something of a massive undertaking both in scope and in financial outlay. I must give a great deal of thanks to my advisor, Donald C. Rhoads, Department of Geology and Geophysics, Yale University, who supported the pilot study in 1971, and who provided unfailing assistance during the continued and expanded project. Robert B. Gordon, Department of Geology and Geophysics, Yale University, was of great help to the project, since it was through him that most of the physical data was obtained.

Peter L. McCall, my research partner, was the initiator of the project, and was the contributor of many of the ideas that appear in this paper. He also designed much of the experiment, and wrote most of the computer programs used for data analysis. J.B.C. Jackson contributed many of the ideas used for selection of experimental plot sizes and predator screens vs. no screens experiment. My thanks also to Tom Ryer who designed the anti-drag structures for the large experimental plots and aided in SCUBA operations

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This Report is Dedicated to Lib

" ... yet how far both of them come
of the truth may be somewhat perceived
by the draught which I have added of
it ... but much better by the Reader's
diligently observing it himself, at
a convenient time ... "

Robert Hooke, Observation LX. Of the Moon
Micrographica, 1665.

INTRODUCTION

When an area of bottom is disturbed by natural or man-induced events so that its 'equilibrium' species composition is radically altered or eradicated, it becomes available for recolonization by adults of motile species and planktonic and swim-crawl larvae of both motile and sessile species. The order of appearance of species on the open bottom area is a function of the potential colonizing species' motility, availability (reproductive strategy and potential, seasonality) and the extent to which the species are attracted to and can survive on the disturbed area.

The colonization may involve changes of species composition as the environment is modified directly and indirectly by biotic and abiotic factors. This primary succession is well described for terrestrial plants. When an area of ground is open to colonization, a pioneer assemblage of plants, adapted to survive in the conditions existing in the open area, enter and modify the previously open area for later colonization. (e.g. Shade intolerant tree species enter an open area and modify the previous environment so that shade tolerant - sun intolerant species are able to colonize. (Horn, 1971))

In the marine environment, there have been few opportunities to study colonization and succession, Brandt(1897); Shelford et. al.(1935); Wilson(1958); Raish(1961); Stone(1963);

Pfitzenmeyer(1970); Howell and Skelton(1970); Pearce(1970); Pratt(1972). These studies have been primarily concerned with the effects of dredging and spoil dumping on the ecology of benthic communities. They are valuable as a first step toward characterizing colonization and succession in the benthos, but they must necessarily deal with relatively uncontrolled, large - scale events, and are thus limited in their ability to produce accurate, predictive knowledge of benthic recolonization and succession. More quantitative and predictive studies of colonization and succession in terrestrial and marine environments have been conducted by Simberloff(1969); Simberloff and Wilson(1969); and Johnson(1971).

The study described here uses the technique of artificially manipulating bottom conditions in the field to study the effects of such changes on the resulting structure and function of the populations in the community.

Until recently, a major task of marine benthic ecology has been to delimit groups of animals which regularly occur together(these groups of recurring species are called communities)and relate their distribution and abundance to prevailing hydrographic and sedimentologic factors. These studies are an important first step in discovering what variables control the distribution and abundance of the marine benthos, and continue to be of importance in relatively unstudied environments such as the deep sea and the Antarctic. These studies, however, are only able to explain factors

operating on relatively large scales. Beyond this their chief value lies in determining the bounds within which further study should take place.

New and more precise knowledge is required to explain the mechanics of the relationships between the environment and the distribution and abundance of the marine benthos. Knowledge of predictive value requires detailed study in restricted areas using new techniques of study and data collection. The project described here is a quantitative experimental study of the effect of different bottom conditions on the ecologic structure and population dynamics of a macrofaunal bottom community in Long Island Sound.

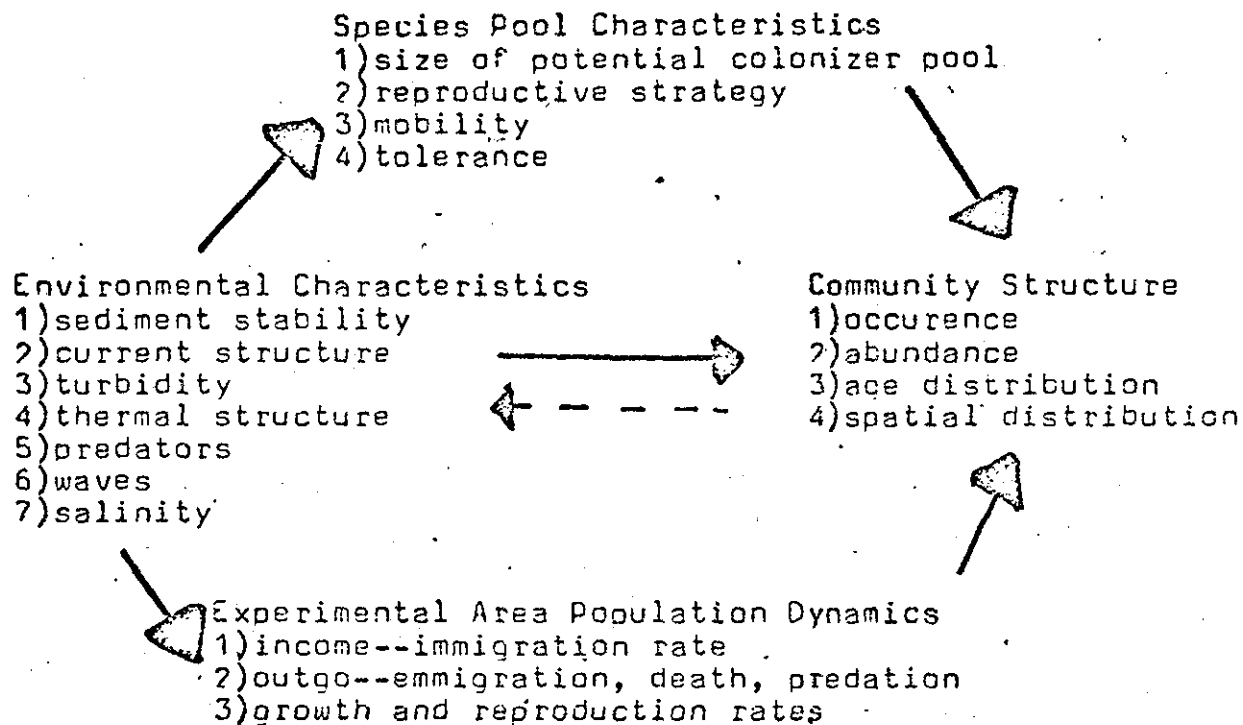
It is the purpose of this study to measure and evaluate the effect of various biotic and physical-chemical factors on the structure and function of the populations in an experimental Long Island Sound bottom community.

Possible important environmental factors and their hypothetical relation to the structure and function of the community are illustrated in Figure 1.

It is implied in the graphical model and herein hypothesized that many of the population changes in estuarine environments are in fact colonization processes. Partly due to climactic variability and to its shallow, enclosed, nearshore position, Long Island Sound is a highly stressed environment (see Slobodkin and Sanders, 1969). The bottom communities must continually recover from local natural and man - induced disturbances. Preliminary results indicate

FIGURE 1

ENVIRONMENTAL FACTORS AND THEIR HYPOTHETICAL RELATION TO
THE STRUCTURE AND FUNCTION OF THE COMMUNITY



ENVIRONMENTAL FACTORS AND THEIR HYPOTHETICAL RELATION TO THE
STRUCTURE AND FUNCTION OF THE COMMUNITY

that this recovery approximates a successional process. In addition, the marked seasonality of these waters requires many species to conduct annual recolonization of the bottom from an overwintering 'remnant' population.

GEOGRAPHIC AND GEOBIOPHYSICAL BACKGROUND

Long Island Sound, together with neighboring embayments to the north, constitutes a characteristic boreal, nearshore, marine environment. Long Island Sound is approximately 90 miles long and averages 15 miles in width with a total area of about 930 square miles. Most of the Sound is less than 30 meters deep. The annual temperature range is 23°C ($2^{\circ} - 25^{\circ}\text{C}$), and the normal seasonal salinity flux is about 4 o/oo ($25\text{ o/oo} - 29\text{ o/oo}$). A small thermocline is present from February - March until August, while a vertical salinity gradient exists throughout the year (Riley, 1956). Inshore areas exhibit a more thoroughly mixed regime with little if any thermal or salinity stratification (Gordon, Turekian, and Rhoads, 1972). A summary of the seasonal surface temperature and salinity conditions (1952 - 1953) is given in Figure 2.

Although it is a more brackish body of water, Long Island Sound shares its major biofacies with the northward Buzzards Bay (salinity about 35 o/oo) (see Rhoads and Young, 1970 for a review of the biologic literature of Buzzards Bay). The important work on the distribution of bottom communities

FIGURE 2

SEASONAL CHANGES IN SURFACE TEMPERATURE AND
SALINITY IN LONG ISLAND SOUND (from Riley, 1956)

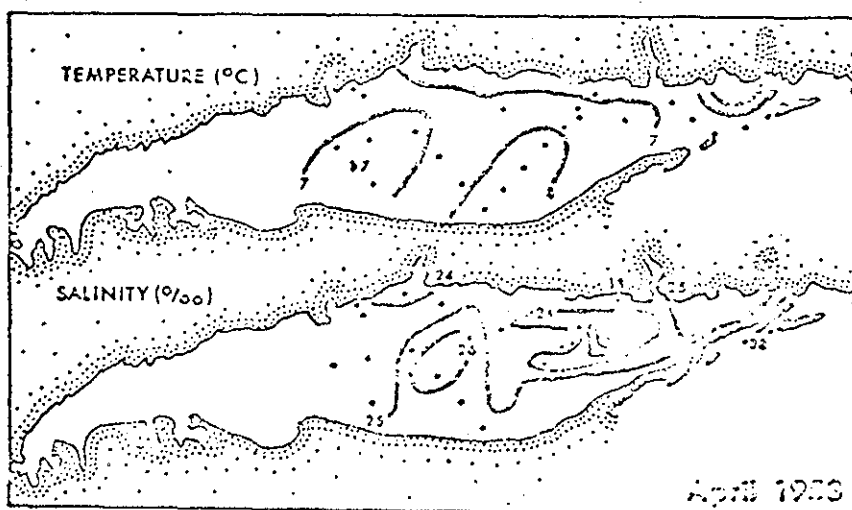
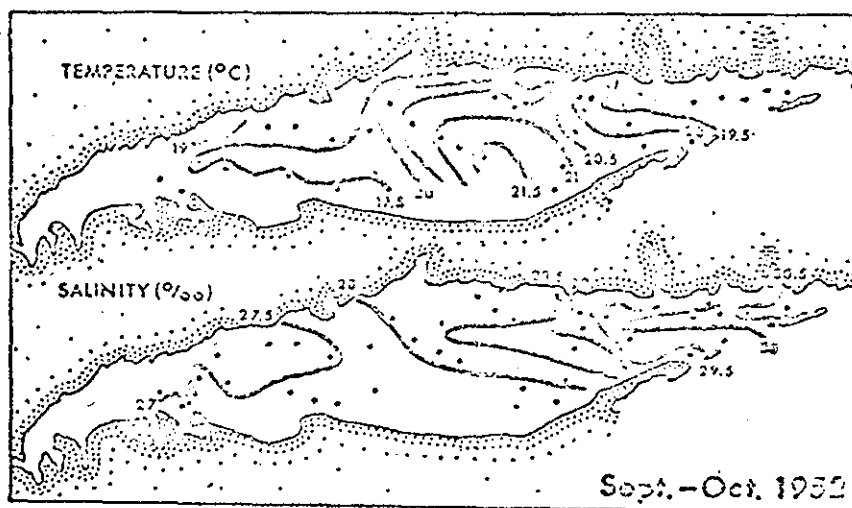
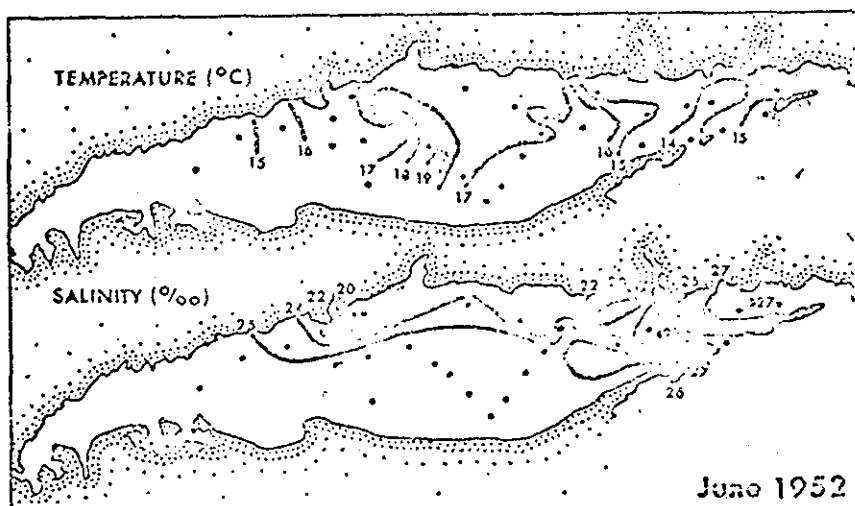


Fig. 1. Seasonal changes in surface temperature and salinity in Long Island Sound. (from Riley, 1956).

has been done by Sanders(1956,1958,1960) and also Buzas (1965). Rhoads(1963,1967,1970,1971,1973) has conducted transect studies and more detailed examinations of animal - sediment relations in this environment.

STUDY AREA

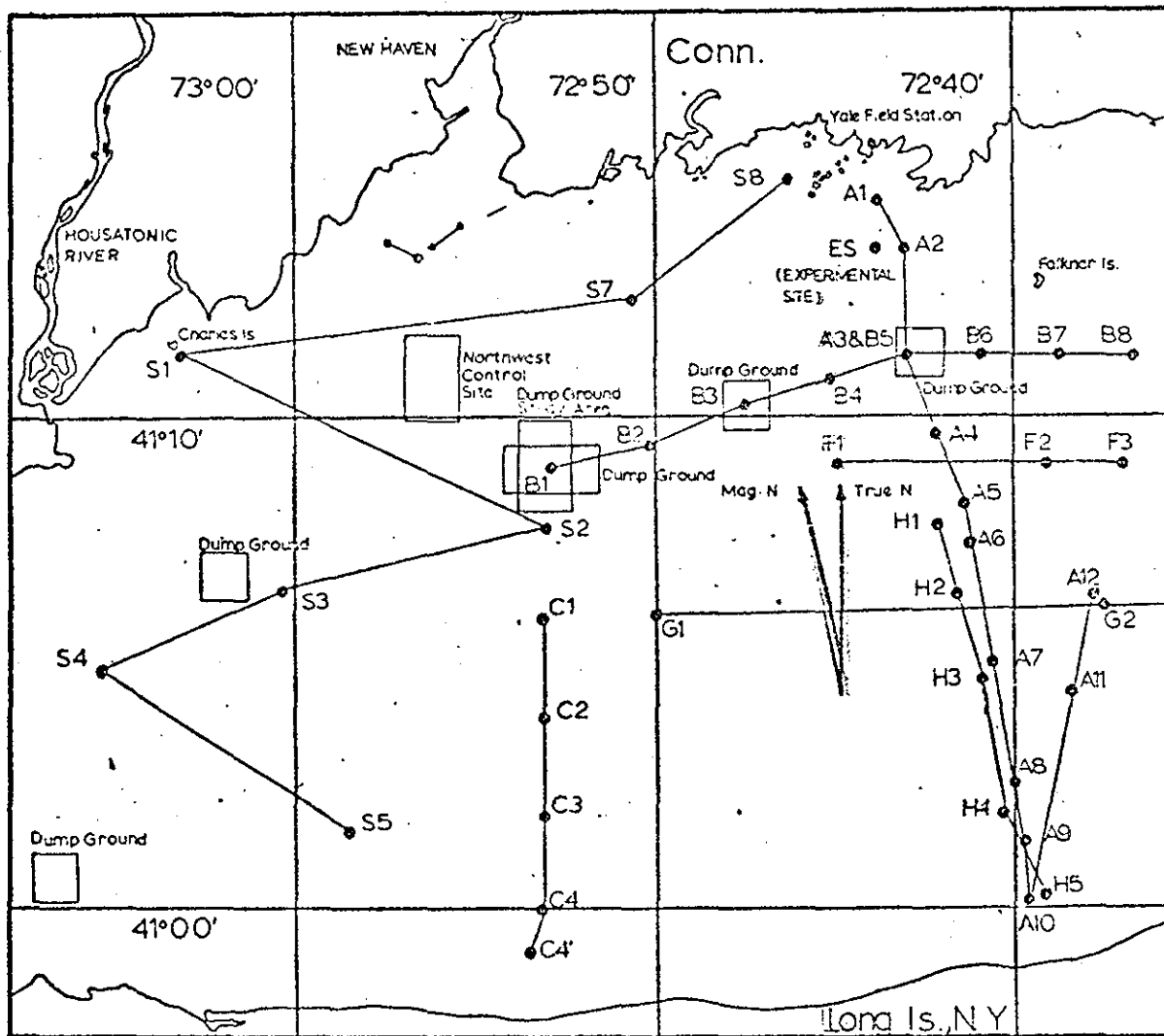
Figure 3 shows the location of the experimental station and grab sampling stations occupied to date. The table following lists the vital statistics of the grabs taken.

The site of the recolonization experiment is located at $41^{\circ} 13.32' N$ $72^{\circ} 44.16' W$, approximately two miles from the Connecticut coast, at a depth of 12 meters (Mean Low Water).

The surrounding bottom material is composed primarily of very fine sand and silt; the clay constituency is approximately 2 % by weight, and non-calcareous coarse-grain material is predominately mica platelets. The dominant coarse material, bivalve shell fragments, are often found exposed on the sediment surface. Direct observations by SCUBA divers indicate that the bottom material is fairly cohesive beneath the thin (2 - 5 cm.) top layer which is composed of fecal pellets.

Direct diver observations and photographs of the sediment surface show the surficial markings to be generally physically produced. Erosional features such as scour marks

FIGURE 3
LOCATION MAP OF STUDY AREA



STATION	VESSEL	DATE	LATITUDE	LONGITUDE	GEAR	#SAMP	DISP.
ES01	Ecos II	7/77/77	41° 13.37	77° 44.16	.147 m ² van Veen	1	Completed
ES02	"	8/9/77	"	"	"	"	"
ES03	Hotspur	9/9/77	"	"	"	"	"
ES04	"	10/13/77	"	"	"	"	"
ES05	"	17/7/77	"	"	.075 m ² van Veen	4	"
ES06	"	7/24/73	"	"	"	"	"
AO1	Ecos II	8/16/77	41° 14.5	77° 43.7	.147 m ² van Veen	1	"
AO2	"	"	41° 13.4	77° 43.0	"	"	"
AO3	"	"	41° 11.2	77° 43.0	"	"	"
AO4	"	8/21/77	41° 09.7	77° 42.3	"	"	"
AO5	"	"	41° 08.3	77° 42.4	"	"	"
AO6	"	"	41° 07.5	77° 41.7	"	"	"
AO7	"	"	41° 05.1	77° 40.7	"	"	"
AO8	"	"	41° 02.6	77° 40.1	"	"	"
AO9	"	"	41° 01.4	77° 40.0	"	"	"
A10	"	"	41° 00.0	77° 40.5	"	"	"
A11	"	"	41° 04.5	77° 41.6	"	"	"
A12	"	"	41° 06.4	77° 42.7	"	"	"
EO1	A.E. Verrill	1/10/73	41° 09.0	77° 57.9	.075 m ² van Veen	4	"
EO2	"	"	41° 09.5	77° 57.9	"	"	"
EO3	"	"	41° 10.3	77° 47.6	"	"	"
EO4	"	"	41° 10.8	77° 45.0	"	"	"
EO5	"	"	41° 11.2	77° 43.0	"	"	"
EO6	Hotspur	7/24/73	"	77° 40.9	"	"	"
EO7	"	"	"	77° 38.7	"	"	"
EO8	"	"	"	77° 36.7	"	"	"
CO1	A.E. Verrill	3/26/73	41° 06.0	77° 53.1	.075 m ² van Veen	4	Unfinished
CO2	"	"	41° 04.0	"	"	"	"
CO3	"	"	41° 02.0	"	"	"	"
CO4	"	"	41° 00.0	"	"	"	"
CO5	"	"	40° 59.2	"	"	"	"
FO1	"	3/27/73	41° 09.1	77° 45.0	.075 m ² van Veen	4	"
FO2	"	"	"	77° 41.0	"	"	"
FO3	"	"	"	77° 37.0	.147 m ² van Veen	1	"
GO1	"	3/30/73	41° 06.0	77° 33.1	"	"	"
GO2	"	"	"	77° 37.3	"	"	"
GO3	"	"	"	77° 50.0	"	"	"
HO1	"	3/29/73	41° 07.7	77° 47.0	"	"	"
HO2	"	"	41° 06.0	77° 41.5	"	"	Completed
HO3	"	"	41° 03.9	77° 40.7	"	"	Unfinished
HO4	"	"	41° 01.9	77° 40.7	"	"	"
HO5	"	"	41° 00.2	77° 39.1	"	"	"

DISP. = disposition of samples as of 23 April 1973

and sediment streaking are common, and become more pronounced with the onset of winter. (Definite ripple marks were observed on 3 March 1973, but were not observed at the most recent sampling on 3 May 1973.) Various biologic markings such as the tracks and trails of gastropods, echinoderms, and crustaceans, worm and amphipod tubes, bivalve siphonal openings, various burrows, and fecal castings are also found. Large fragments of marine and terrestrial plants are commonly observed passing over the surrounding bottom.

Salinity, temperature, and turbidity measurements (Gordon, Turekian, and Rhoads, 1972) show the experimental site to be subject to a high degree of turbulent mixing. The water column in the area exhibits no summer pycnocline, thermocline, or pronounced turbidity stratification. The absence of a density gradient and the presence of tidal mixing indicate that the experimental site is subject to major salinity changes resulting from major rainfall events such as Hurricane Agnes which resulted in an influx of freshwater comparable in magnitude to a second spring runoff event (pers. comm. Larry Benninger, 1972).

Wave action during storms is also important, since the experimental site is in shallow water such waves are a powerful agent for erosion and resuspension of bottom material.

Tidal current velocity profiles obtained from the experimental sites by means of a Price current meter exhibit a typical logarithmic form. Observed bottom velocities ranged from 3 to 5 cm./sec.

EXPERIMENTAL DESIGN

The goal of this project is the thorough documentation of the colonization process and succession of macrobenthic organisms on an artificial bottom area. An experimental design was chosen that successively subtracts effects due to the presence of other organisms in the community (PLOT I), predators (PLOT II), waves and currents (PLOT III), and temperature (PLOT IV). It was also desired to sample the natural bottom at the experimental site (PLOT V) to follow natural changes in the biology and sedimentology at the site.

Plots I and II consist of 11' x 13' shallow wooden boxes which were constructed onshore and into which 100 0.1 m² azoic mud sediment containing plastic pans were placed. With flotation attached, the apparatus was towed to the experimental site and sunk. Plots I and II originally consisted of six of these 100 sample units. Two of these are assigned to Plot II and are covered with $\frac{1}{4}$ " galvanized hardware cloth to exclude predators. At present, these anti-predator screens have been removed by wave and tidal action. They will be replaced by more substantially constructed screens in late May 1973. The remaining four 100 sample units are assigned to Plot I. Two of these units are being randomly sampled at regular intervals. The remaining two are being used to document long term effects and are not to be disturbed for 12 to 15 months from the initiation of the experiment (27 July 1972). One of the long term 100 sample units was lost soon after emplacement and is presently missing.

Plot III is a 100 sample unit established in an onshore

aquarium to remove the effects of waves and tides. The physical facilities are presently constructed, but they have not yet been put into operation.

Plot IV is an additional shorebased 100 sample unit which was to be temperature controlled. This was not completed because it was found to be too costly to construct the necessary heat exchanger.

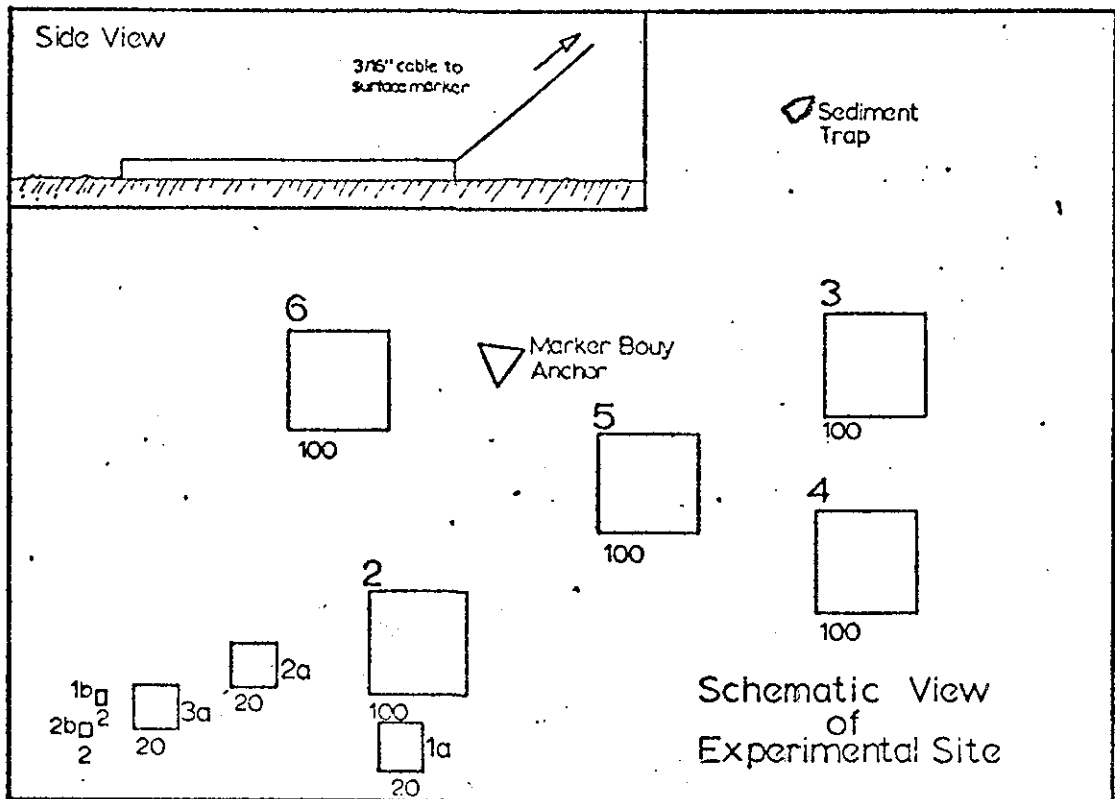
Plot V is the natural bottom area of the Sound. This is being sampled every six weeks in the vicinity of Plots I and II by means of a $.147 \text{ m}^2$ and a $.025 \text{ m}^2$ Van Veen grab sampler to establish the general existing community characteristics of the surrounding mud bottom area. Outlying areas of the Sound's level bottom are being sampled by the same grabs on a seasonal basis (see Figure 3 and table following it for details of grab sampling transects).

Samples from Plots I and II are taken which represent colonization from the beginning of the experiment and colonization of samples replaced at the previous sampling interval.

To test plot size effects, replicate experimental plots $1/5$ and $1/50$ the size of the main experimental plots (20 and 2 units respectively) have been emplaced on the study site and will be sampled at the end of the 12 to 15 month period for comparison with the larger main plots..

It was observed that when the $\frac{1}{2}$ " screens were in place on the experimental plots there was increased sediment accumulation in the sample pans. When the anti-predator screens are replaced $\frac{1}{2}$ " screens will be used to negate this effect if possible. Figure 4 is a schematic of the offshore experiment.

FIGURE 4
SCHEMATIC VIEW OF EXPERIMENTAL SITE



DETAILED METHODS

CONSTRUCTION OF OFFSHORE PLOTS: The six 100 sample unit plots are 11' x 13' shallow wooden boxes constructed of 2 x 6 plank framing and 3/8" plywood flooring with 2 x 4 reinforcing members. The plastic sample pans placed in the plots were filled with defaunated mud dredged from the Yale Biological Field Station harbor, Old Quarry Road, Guilford, Connecticut. Defaunation (for macrofauna) was accomplished by permitting the mud filled sample pans to dessicate in the sun for a period of from one to two weeks. Fresh water was added to the mud at the end of the defaunation period to reconstitute the physical properties of the mud.

The smaller, area effect, plots are identical in construction to the large plots but are respectively 1/5 and 1/50 their size. At present three 1/5 and two 1/50 size plots are in operation at the experimental site.

LOADING PROCEDURE: To prevent washout during towing and sinking, and to prevent premature faunal settlement, each of the plastic sample cells was covered with 6 mil. black polyethylene sheeting. These covers are secured to the sample cells by means of elastic bands fabricated from truck tire inner tubes. The covered sample cells were then loaded onto the plot boxes and secured in place by passing 16 gauge steel wire through the plastic tray handles and attaching the wire to the sides of the plot boxes. The loading procedure was carried out with the wooden plot boxes alongside the field station dock or aground below the high tide line since

no facilities were available for handling the great weight of the loaded plots(4000 lbs. for the large units and 800 lbs. for the 1/5 size units)on land.

Flotation for the large plots was provided by three 55 gal. steel drums arranged in a triangular fashion and attached to the plots by 16 gauge steel wire. The 1/5 size units were fitted with two 30 gal. steel drums. All drums were fitted with pipe nipples and end caps to facilitate bouyancy control. The 1/50 size units presented no weight problem and were simply loaded aboard the drop vessel and lowered from the deck at the experimental site.

TOWING: The large and 1/5 size units were originally fitted with eyebolts in their forward corners to which a towing bridle was attached. This arrangement proved to be unsatisfactory and later tows used 1" holes drilled in the forward corners of the units for attaching the towing bridle.

After the first tow and drop attempt it was found necessary to provide the units with detachable drag reducing structures.

EMPLACEMENT: After coming on station, the drop vessel made fast to the experimental site bouy, and the sample unit to be emplaced was brought alongside. At this time the drag reducing structures were removed and the descent bridle was attached to eyebolts at each of the units four corners. The descent bridle was then attached to the drop vessel's winch line. At this point three divers entered the water

to begin flooding the flotation drums. This flooding was conducted under the supervision of a 'drop-supervisor' to assure plot trim during descent. When a slight negative bouyancy was achieved, and the trim of the plot was confirmed, the unit was permitted to slowly descend.

After the plot reached the bottom, a team of SCUBA divers dropped down the attached winch line to secure a marker bouy to the plot. After this was accomplished, the divers cut the flotation drums free and attached them to the drop vessels winch line and detached descent bridle. After the divers had returned to the surface the drums were hauled aboard the drop vessel for future use.

INITIATION OF EXPERIMENT: When all plots had been emplaced on the experimental site, SCUBA divers removed the steel wire sample cell retainers and sample cell covers. All of this material was collected in mesh bags and returned to the surface for disposal on shore.

The predator screens, which were constructed of 2 x 2 framing and $\frac{1}{2}$ " galvanized hardware cloth were emplaced at this time. This arrangement proved to be extremely flimsy and the screens were very quickly destroyed by wave and current action. These are to be replaced in May 1973 with more substantial materials as described earlier.

SAMPLING: Although the original experimental design specified the removal of two samples from each of the screened and unscreened continuously sampled plots, this plan was modified by various technical considerations such that two

samples were removed at each sampling interval from one originally unscreened plot. The samples removed were replaced by azoic sample cells, and one of these was removed at the next sampling interval to record recolonization during the elapsed time between sampling intervals. The samples to be recovered were chosen randomly.

Recovery of samples was accomplished by SCUBA diver. The diver located the desired samples by means of numbers and letters painted on the sides of the plot, removed the samples and covered them to prevent washout.

After reaching shore, the samples were fixed and stained in a solution of 3 % formalin and 10 % rose bengal. This stain permits more rapid sorting of the animals in the sample. After three days in the fixative stain, the samples were sieved through a 250 micron mesh, and the matter retained was preserved in 95 % methanol. The animals were removed from this material under a dissecting microscope and identified to species if possible. The identification procedure involved the use of standard invertebrate keys for the region (Gosner, 1971; Smith, 1964 etc.), consultation with taxonomic experts, and comparison with known specimens from the Bingham Oceanographic Collection. The identified animals are stored in 95 % methanol for later measurement, biomass determination, and chemical analysis.

CORING PROGRAM: A series of twelve cores is taken at each sampling interval. Six from the surrounding bottom and six from inside the plot sample cells. These are later analyzed for water content with depth. All cores are taken by hand. A sediment reworking experiment is also cored for X-ray analysis.

LARGE EXPERIMENTAL PLOTS UNDER CONSTRUCTION AT YALE
FIELD STATION

MOVING LARGE PLOT TOWARD WATER. THE LARGE SIZE OF THE
PLOTS MADE THEM VERY DIFFICULT TO HANDLE

PREPARING TO TOW EXPERIMENTAL PLOTS FROM YALE FIELD STATION
HARBOR TO EXPERIMENTAL SITE

TOWING PILOT STUDY PLOT -- BUZZARDS BAY, MASS. 1971.

PILOT STUDY PLOT BEING MADE READY FOR DESCENT -- BUZZARDS
BAY, MASS 1971.

SEDIMENT TRAP: To document the resuspension rate at the experimental site the apparatus shown in the following plate was built and emplaced on station on 15 August 1973. The trap is constructed of 2 x 4 lumber and 3/8" plywood. The base of the trap contains approximately 300 lbs. of concrete to maintain stability and the central 2 x 4 shaft is secured by means of 3/16" stainless steel cable tightened by turn-buckles.

The suspended sediment is collected by means of eight 1 at. screw top glass jars arranged in pairs at .15, 1, 2 and 3 meters above the bottom and secured to the cross members of the trap by elastic bands. These jars are collected at each sampling interval by a SCUBA diver. The bottles are capped before removal to prevent washout, and fresh jars are secured to the trap by the diver. In the lab the sediment is dried and weighed and analyzed for grain size composition.

HYDROGRAPHIC VARIABLES: Current profiles, temperature, salinity and turbidity measurements at and around the experimental site were made by a work crew under the direction of Robert B. Gordon, Department of Geology and Geophysics, Yale University.

Current measurements were made by a Braincon type 381 film recording histogram current meter bottom - moored to a steel weight secured to a Danforth anchor. The meter was placed 180 cm. above the bottom. (This height is within the zone of active transport of sediment, but is sufficient in height to discourage interference with the meter rotors by motile benthic epifauna) (Gordon, Turekian, and Rhoads, 1972).

SEDIMENT TRAP

Velocity gradient measurements from top to bottom of the water column were made from a moored boat with a Price type current meter. The procedure is to moor the boat at bow and stern and support the meter on a taut wire running to a weight set on the bottom. Electrical pulses generated by rotation of the meter bucket wheel are indicated on a strip chart recorder; current speed is found by counting the pulses recorded over a fixed time interval using the manufacturer's calibration data for the meter. (Gordon, Turekian, and Rhoads, 1972).

Turbidity profiles were made with an optical transmissometer built in the Yale Geology and Geophysics laboratory. The transmission of white light through a 10 cm. column of water is measured by this instrument. An attached thermister records temperature.

Salinity profiles were taken by means of an induction salinometer (Hydro Products, San Diego, Calif.)

FAUNAL SURVEY PROGRAM: In order to have a better understanding of the benthic biology of Long Island Sound, a transect sampling program was undertaken to determine large scale faunal distribution, seasonal effects, and sedimentology. These samples were treated in the same manner as those from the experimental plots. A subsample was removed from each sample and analyzed for grain size composition. This material was decalcified with .1 N HCl and allowed to dry after rinsing. The dry material was then pulverized and subjected to sieving and pipette analysis. The analysis of the sediment from

the sediment trap experiment were not decalcified before sieving and pipette analysis as the size and amount of shell material was of interest.

Additional data on small scale faunal distribution was collected by work parties under the direction of Donald C. Rhoads, Department of Geology and Geophysics, Yale University from the New Haven dredge spoil dump site and surrounding areas (see Figure 3). All of these samples were collected by means of a .147 m² Van Veen grab operated from the U. S. Army Corps of Engineers tug, Manamet.

HABITAT DOCUMENTATION: Diver photographs and observations are available for the experimental site, Station A3 (Guilford dredge spoil dump site), New Haven dump site, and Northwest Control site. These are of great value in the environmental interpretation of the Long Island Sound mud bottom. These photographs were made by a 35 mm reflex Nikomat camera in an Al Giddings U/W housing using a Strobosnar flash unit and by a 35 mm Nikonos using the same flash unit. The subject to lens distance is about 30 cm in all cases.

DATA ANALYSIS: All faunal data was keypunched on cards and keyverified. Processing and plotting of the faunal data was done on the Yale IBM 370 and IBM CALCOMP plotter. Mapping of small scale faunal distribution from Rhoad's data for the molluscs at the Northwest Control site was done by means of an overprinting program. Diversity determinations were made using the Brillouin formula for information bits per individual.

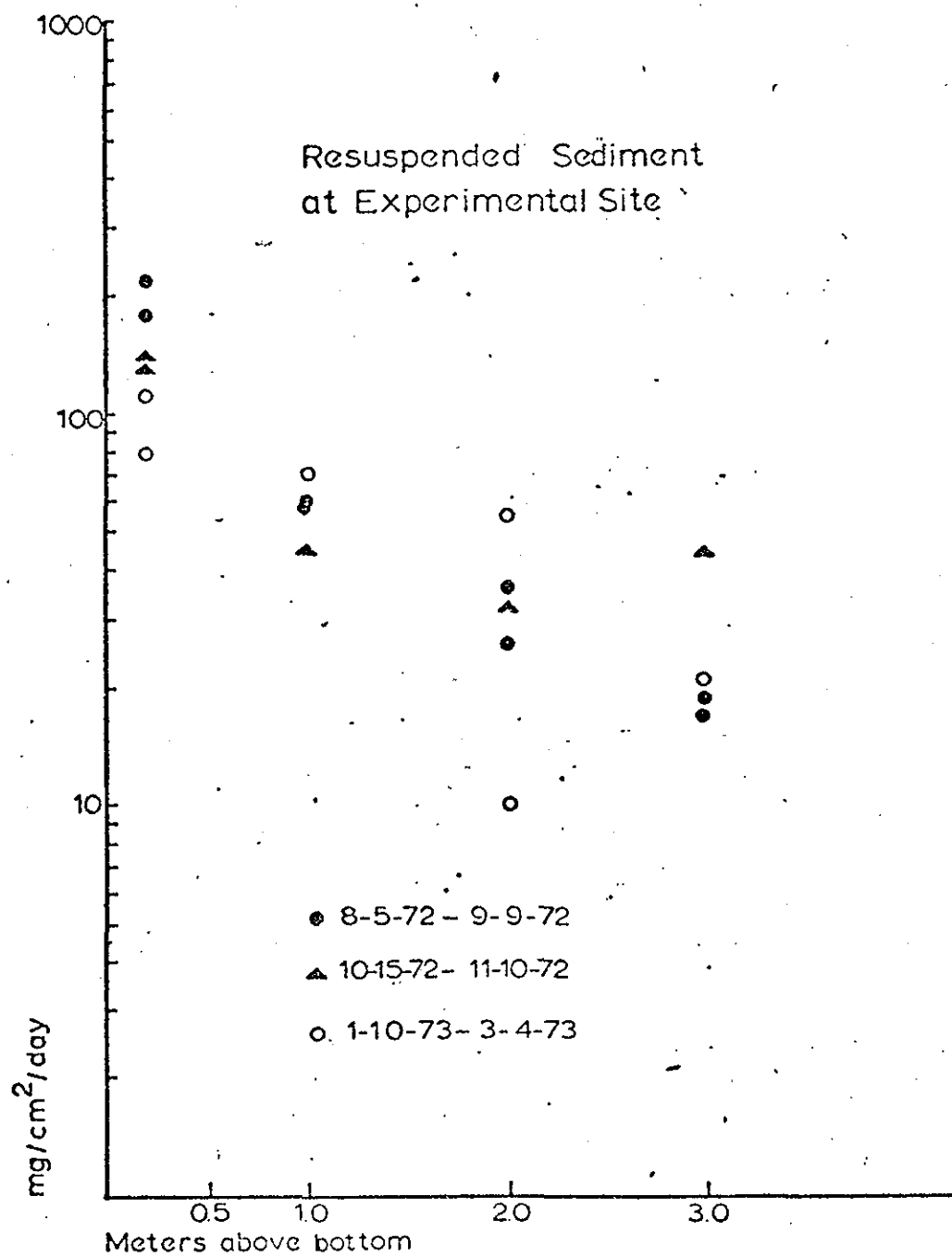
ALIUQUOTING PROCEDURE: The extremely large numbers of small polychaete worms and amphipods present in the samples from the experimental plots necessitated aliquoting of the total samples. The entire sample was weighed and a subsample of approximately five grams was removed (the exact weight was determined in each case). All organisms in the aliquot were counted. The total abundance of the numerous small polychaetes and amphipods was then determined to within 5 % by scaling the values obtained from the aliquot to the total sample weight. Larger organisms were counted for the entire sample.

RESULTS AND DISCUSSION

I. The Physical Environment

The experimental site, being an inshore area, is subject to a high degree of environmental stress. Tidal turbulence dominates the physical environment since it is the most important agent for resuspension of sediment and bottom erosion. Suspended sediment values for the site determined by means of a sediment trap apparatus are quite high. The .15 m. level of the sediment trap gives values ranging between 100 and 200 mg./cm²/day (see Figure 5). These values are approximately an order of magnitude greater than those obtained for a subtidal environment in Buzzards Bay, Massachusetts by Young (1971). There appears to be a slight seasonal variation apparent at the .15 m. level with higher values appearing during warm conditions and smaller values

FIGURE 5
RESUSPENDED SEDIMENT AT EXPERIMENTAL SITE



during cold conditions. This would be expected since less sediment is reworked by organisms during the winter due to their reduced metabolism. The distinction of higher values vs. lower values for seasonal change is not at all clear from higher levels of the sediment trap. I would attribute this to lack of experimental replication due to lost trap bottles. It is also conceivable that higher current velocities at higher elevations above the bottom altered the amount of sediment retained.

Wave action during storms and high winds is a very important factor for sediment resuspension of sediment and bottom erosion. Waves are able to erode and resuspend much larger particles than normal tidal currents. A storm event in late November or early December 1972 deposited shell fragments which were 1-2 cm. in width in the .15 m. level of the sediment trap. Wave stress on the bottom is an aperiodic effect and cannot be accurately predicted, however it is evident that it is an extremely important environmental stress. Really major storm events on the sound which are recorded in the sedimentary record as major storm deposits have an apparent periodicity of approximately 30 years from radiometric dating (Gordon, Turekian, and Rhoads, 1972).

The highly physical nature of the environment of the experimental site is recorded in the surficial features of the bottom as described earlier. The experimental site differs from offshore (25 - 30 meters MLW and deeper) areas in this respect. The offshore regions although under intense physical stress are apparently less affected than inshore regions and

represent a more stable situation. The surficial markings on offshore bottoms are predominately biologic in nature. There is evidence that the offshore bottoms do undergo periodic erosion, however they are obviously not as strongly affected as inshore areas.

The onset of winter and the corresponding temperature decrease causes high mortality in benthic populations and appears to be a very important regulating factor in community structure in all areas of Long Island Sound. The occurrence of more frequent and severe storms in winter accompanied by decreased temperature have a much more powerful effect on inshore areas, and in some instances are sure to have catastrophic effects on inshore benthic populations.

Bottom surficial markings at the experimental site during the winter indicate increased erosion and reduced sediment reworking. The markings resembled ripple marks in form. The erosional face of the marks was covered by shell debris, while the depositional face exhibited finer material (apparently very fine sand and silt). Since substrate characteristics are very important for larval settlement and recruitment such large changes in the nature of the substratum due to large erosional events during the winter must be of great importance in determining community structure and environmental patchiness. It was also noted that the bottom material was much more cohesive during the winter as it could not be penetrated easily by a diver's hand.

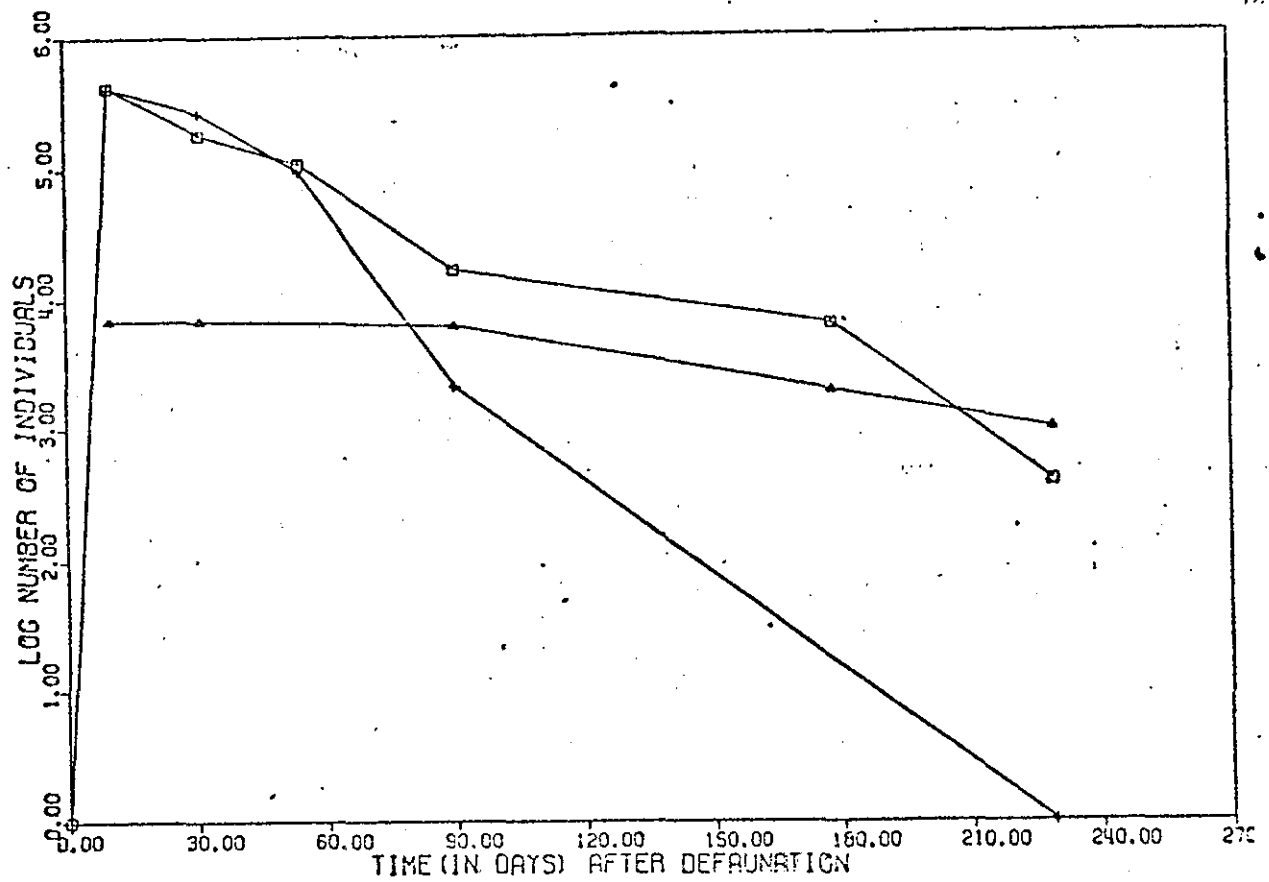
II. Recolonization of the Experimental Plots

The most striking aspect of the recolonization of the experimental plots is the rapidity and intensity with which it occurred. Within 10 days after initiation of the experiment, faunal density on the experimental plots had reached an unexpected level of 500,000 individuals / m^2 compared to 14,000 individuals / m^2 occurring in the surrounding bottom. (See Figure 6). As time progressed, the population density in the experimental plots continued at a high level relative to the surrounding bottom. As can be seen in Figure 6 the population density of the experimental plots continuously decreases and experiences a rapid decline with the onset of winter. Population density values for the surrounding bottom remain at a fairly constant level until winter effect produces a relatively slight decline.

Data from the replacement samples indicates that individuals were arriving on the experimental plots (and presumably on the surrounding bottom) until +90 days. Later values for recruitment of individuals are not as large as those from the late summer.

The number of species present on the experimental plots exhibited an initial burst to 14 species followed by a slow rise to 20 species at +90 days. After this time the number of species present crashed to a low level. (See Figures 7 & 8) The pattern for the surrounding bottom shows a constant number of species over the first three sampling intervals rising to a peak at +90 days and declining thereafter.

FIGURE 6
NUMBER OF INDIVIDUALS OVER TIME

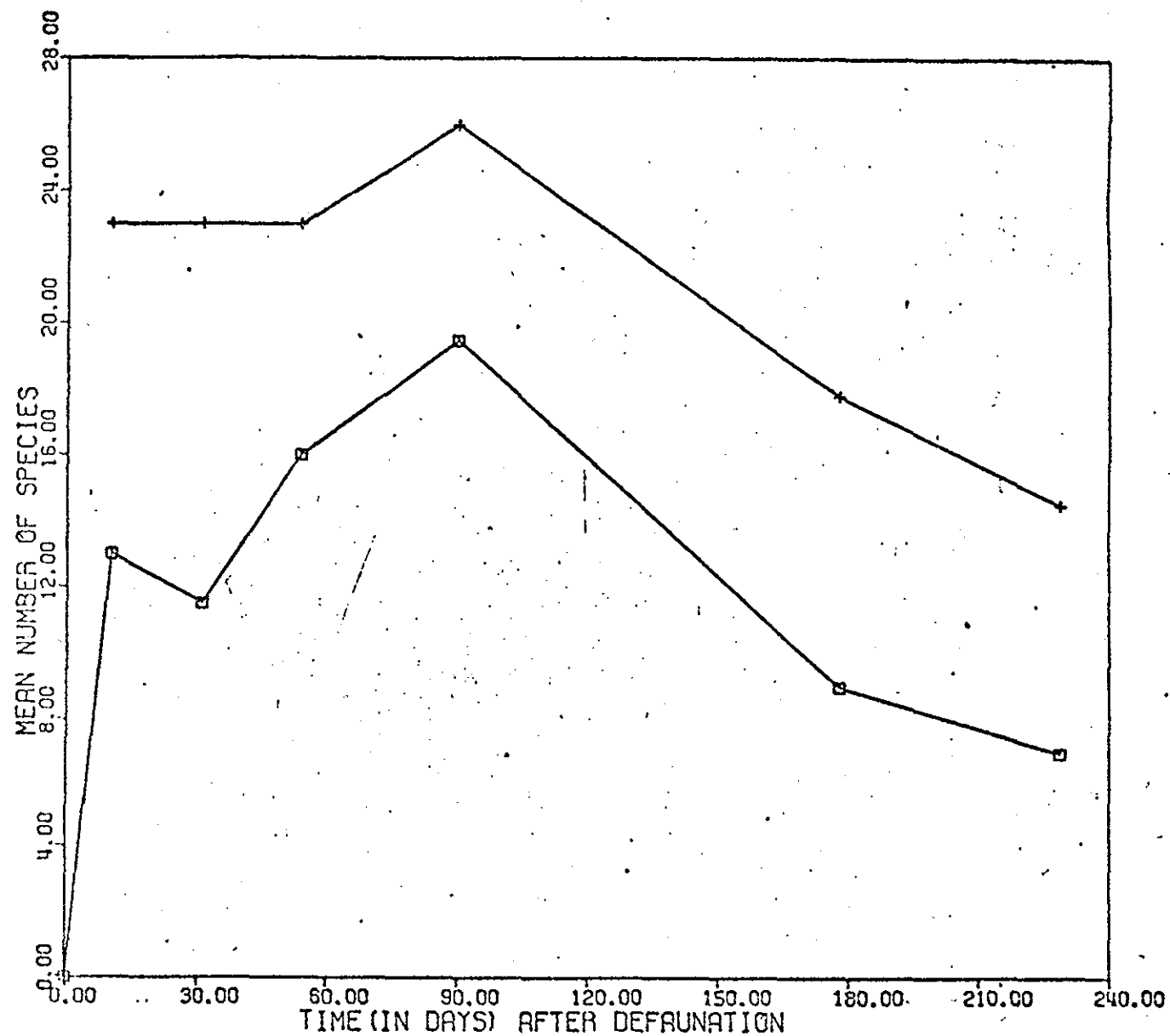


EXPERIMENTAL SITE - INSIDE SAMPLES
EXPERIMENTAL SITE - REPLACEMENT SAMPLES
EXPERIMENTAL SITE - OUTSIDE SAMPLES

FIGURE 7

NUMBER OF SPECIES AT EXPERIMENTAL SITE 7/72-3/73

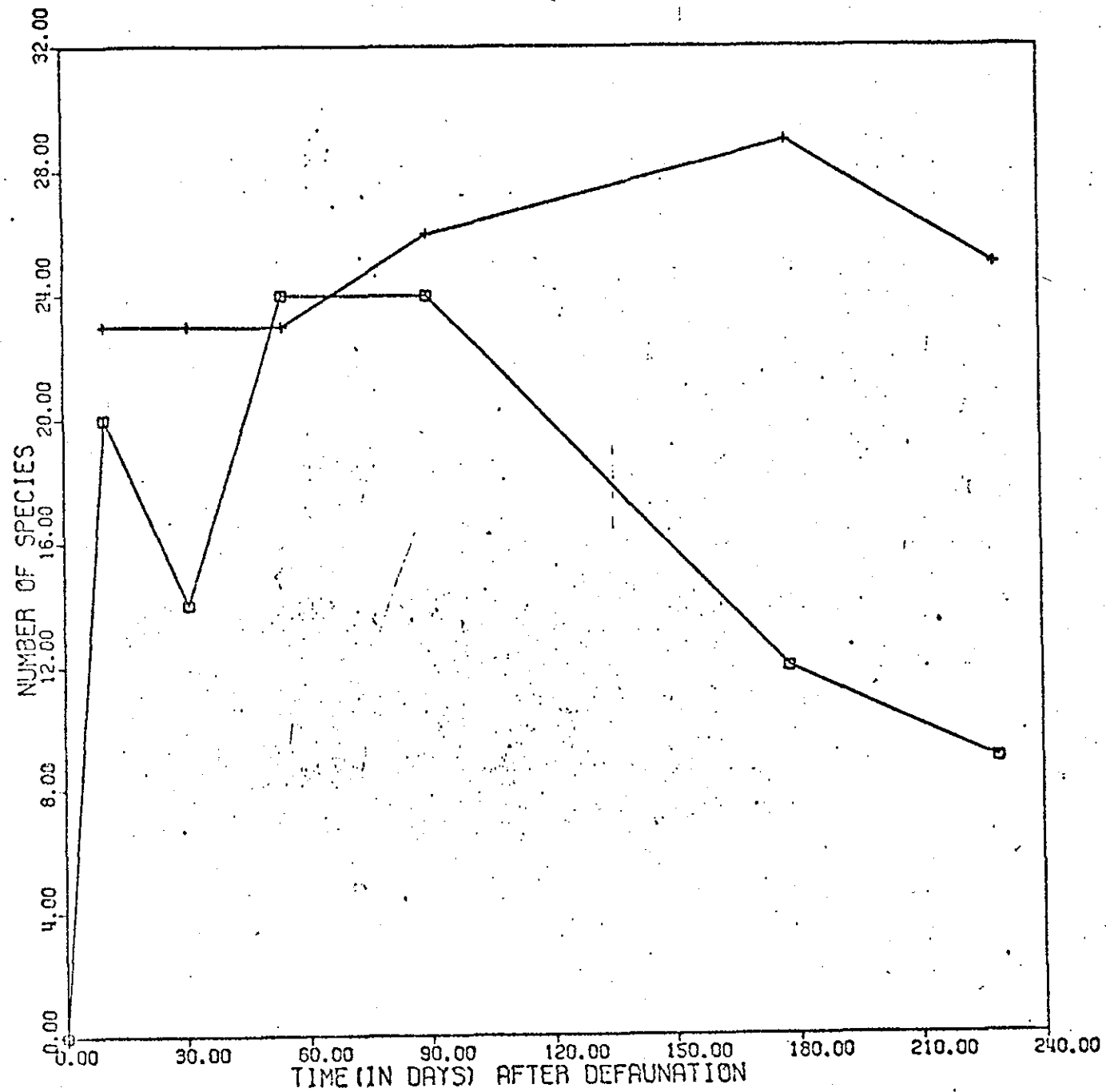
NUMBER OF SPECIES AT EXPERIMENTAL SITE 7/72-3/73



□ EXPERIMENTAL SITE - INSIDE SAMPLES
 + EXPERIMENTAL SITE - OUTSIDE SAMPLES

FIGURE 8
CUMULATIVE NO. OF SPECIES AT EXPERIMENTAL SITE
7/72-3/73

CUMULATIVE NO. OF SPECIES AT EXPERIMENTAL SITE 7/72-3/73



☐ EXPERIMENTAL SITE - INSIDE SAMPLES
☐ EXPERIMENTAL SITE - OUTSIDE SAMPLES

The peak number of species present at +90 days indicates that the extinction rate for newly settling species was low at this time. This is possibly due to reduced predation pressure as very few predators were observed by divers at this sampling interval.

The seasonal mortality effect is operative in both the experimental plots and in the surrounding bottom, but the results are more catastrophic for the experimental plots.

Diversity values over time (See Figures 9 & 10) indicate that the surrounding bottom area has relatively constant diversity levels with a slow rise to a peak value at +180 days. Diversity values for the experimental plots show a sharp rise to a peak value at +90 days and a rapid decrease thereafter. The diversity values for the experimental plots are consistently lower than those of the surrounding bottom. This tends to indicate that the community of the surrounding bottom is "higher grade" than that of the experimental plots.

Equitability ($H/H(\text{Max})$) over time for the surrounding bottom area shows a relatively constant value until +90 days and a rising tendency thereafter. The experimental plots exhibit a rise in equitability until +90 days, a sharp drop at +180 days, followed by a sharp rise at +220 days. The oscillations of equitability in the experimental plots tends to indicate that the plots are more unstable biologically than the surrounding bottom. (See Figure 11)

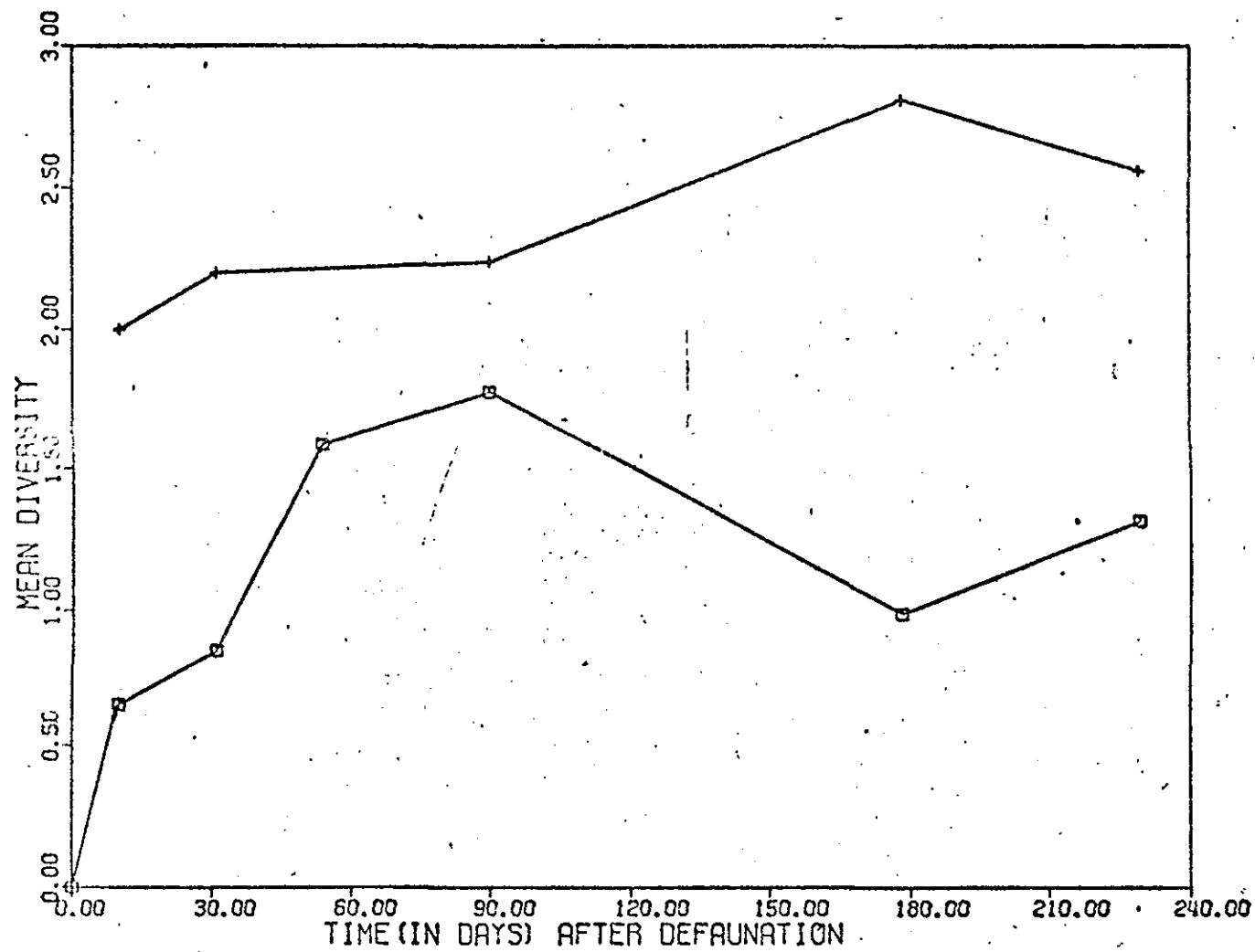
The macro-biologic picture for the experimental plots shows a rapid initial colonization process occurring in late

FIGURE 9

DIVERSITY VS. TIME - EXPERIMENTAL SITE

7/72-3/73

DIVERSITY VS. TIME - EXP. SITE 7/72-3/73



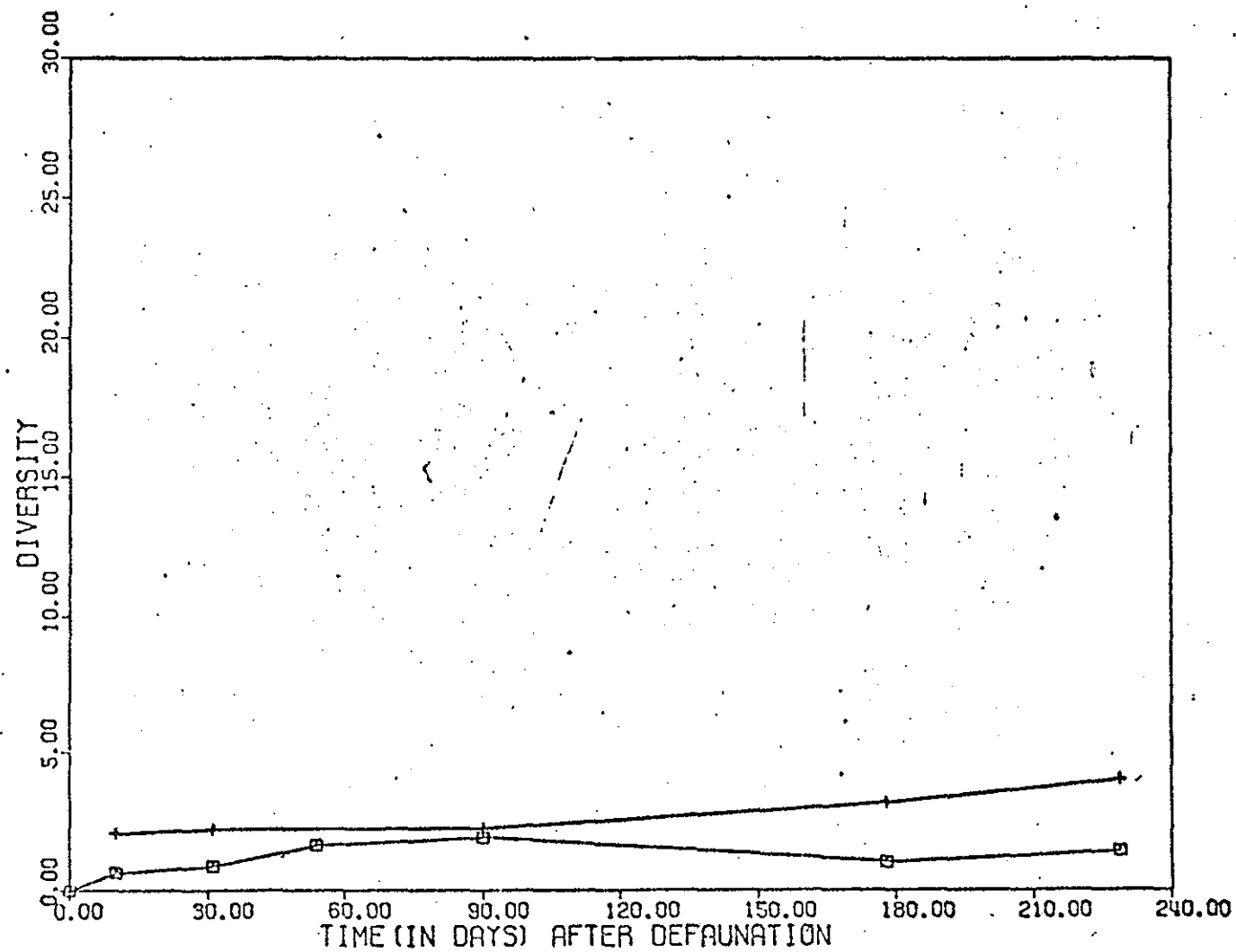
□ EXPERIMENTAL SITE - INSIDE SAMPLES
+ EXPERIMENTAL SITE - OUTSIDE SAMPLES

FIGURE 10

CUMULATIVE DIVERSITY VS. TIME - EXPERIMENTAL SITE

7/72-3/73

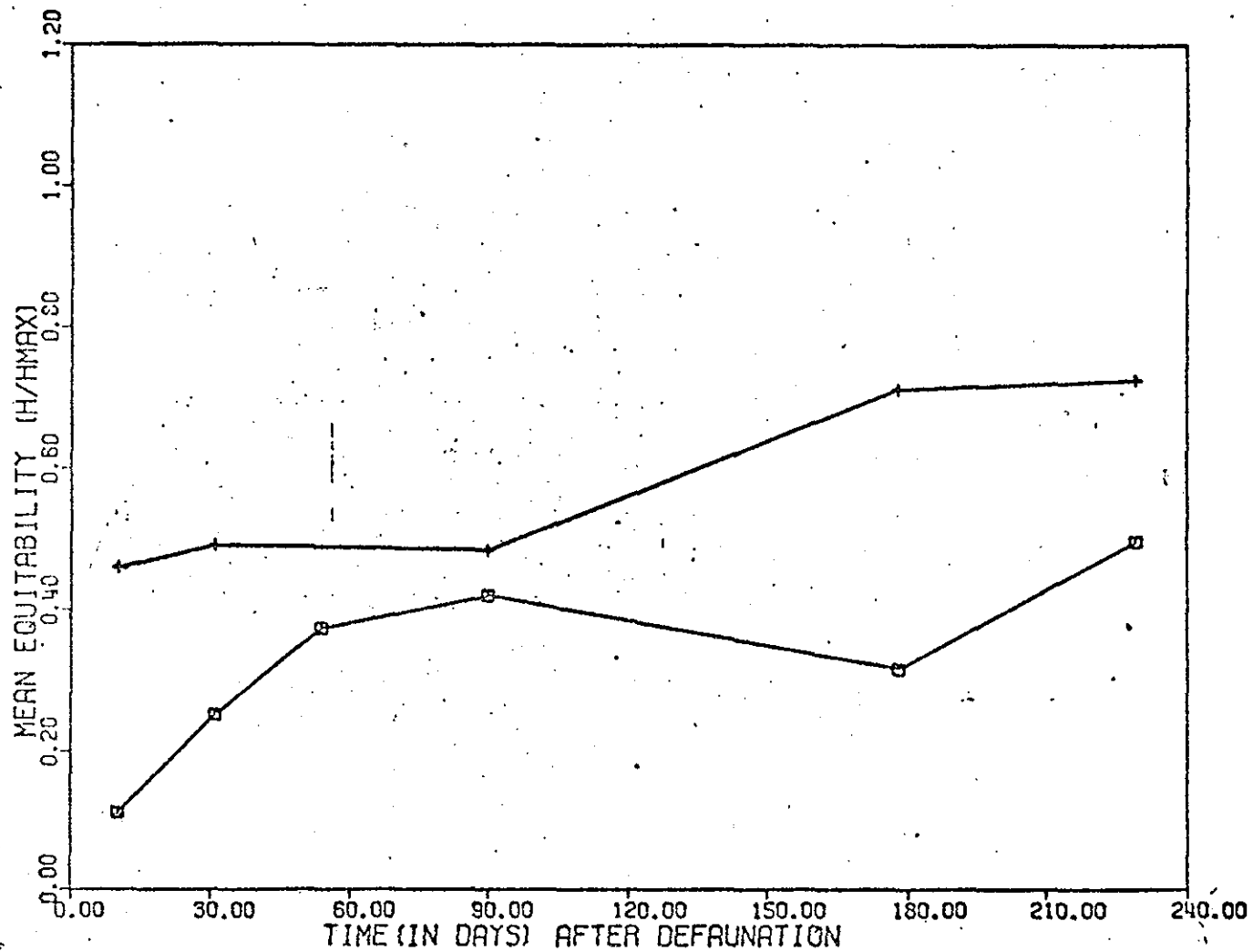
CUMULATIVE DIVERSITY VS TIME - EXP. SITE 7/72-3/73



□ EXPERIMENTAL SITE - INSIDE SAMPLES
+ EXPERIMENTAL SITE - OUTSIDE SAMPLES

FIGURE 11
EQUITABILITY VS. TIME AT EXPERIMENTAL SITE
7/72-3/73

EQUITABILITY VS TIME AT EXP. SITE 7/72-3/73



□ EXPERIMENTAL SITE - INSIDE SAMPLES
+ EXPERIMENTAL SITE - OUTSIDE SAMPLES

summer and early fall followed by a cessation of colonization with the onset of winter and a rapid decline in both population density and species number. The biologic composition of the experimental plot community appears to be unstable and suffers greatly from winter mortality. In contrast, the surrounding bottom community appears to be biologically and physically accommodated, and is much less affected by physical and biologic events.

An attempt was made to apply equations developed by MacArthur and Wilson (1963) to predict \hat{S} (equilibrium species number) for the experimental plots. It was found, however, that the immigration rate of new species was non-linear so the equations could not be applied. The reason for the non-linear nature of the immigration rate in the case of the experimental plots is probably due to the fact that the distance between the plots and the source population is zero.

It is interesting to note here that replacement sample data indicates a lower influx of new individuals as time progresses with a complete shutdown of the influx at +220 days. If defaunation of an area of bottom took place in late fall or winter it appears highly unlikely that sufficient recolonization of the area would occur to stabilize the sediment physically. This means that a soft bottom area defaunated at a time of low or non-existent colonization potential of the surrounding bottom would be subject to intense erosion by waves and tidal currents until a deflation armor of shell debris could be formed by the erosion.

III. Succession or Sequencing in the Benthos

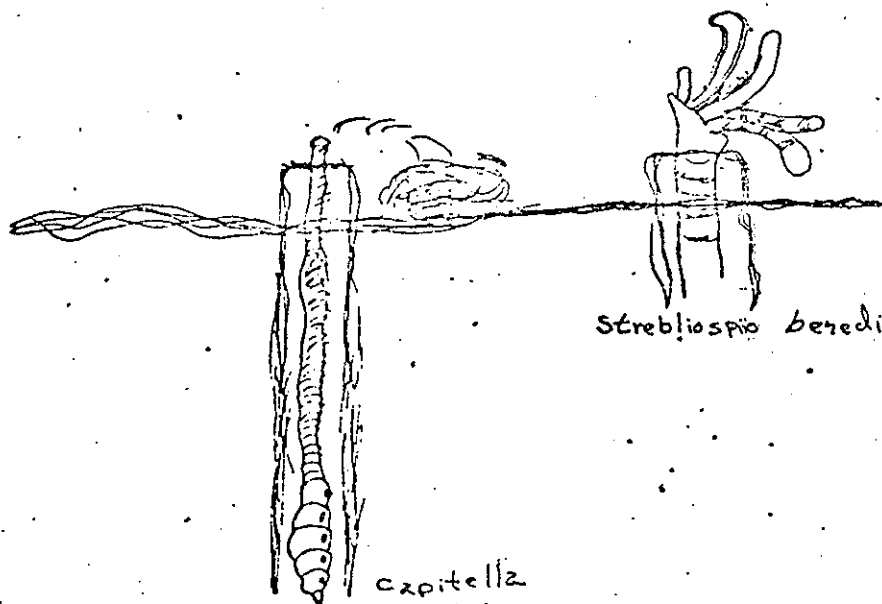
At the first sampling interval over 2/3 of the species and over 95% of the individuals present on the experimental plots were deposit feeders; the majority of these were also tube dwellers. The two most important species, Streblospio benedicti (90.6 - 85.4 % of total individuals) and Capitella capitata (6.7 - 10.5 % of total individuals) are definitely opportunistic species. Both species exhibited extremely high population densities at the initial sampling and both exhibited high mortality over time. In addition, data from the replacement samples shows these two species to consistently be the first colonizers of empty substratum.

Both S. benedicti and C. capitata are tube dwelling, deposit feeding polychaete worms. They differ in that while S. benedicti is a surface deposit feeder, C. capitata feeds on subsurface deposit (See Figure 12). Both species have pelagic larvae (generally--there are some reports that indicate C. capitata has two forms of larvae), and both have wide geographic distribution. These characteristics are indicative of an 'R' type strategy, and, I believe, of first colonizer (first successional or sequential stage) strategy.

Wass(1967) and Dean(1970) have identified S. benedicti as a possible pollution indicating organism. This status of pollution indicator has also been applied to C. capitata (Reish, 1961). C. capitata was also the first specie to

FIGURE 12

LIFE POSITIONS OF STREBLOSPID BENEDICTI AND CAPITELLA CAPITATA



Strebliospio benedicti

capitella
capitata

NOT TO SCALE

settle in areas heavily affected by the West Falmouth, Mass. oil spill(Sanders, Grassle, and Hampson, 1972). It seems more likely that the occurrence of these organisms is an indication of a highly variable environment, as these animals are abundant in unpolluted estuaries where salinity varies 0-10 o/oo, and in salt marshes where salinity is low and variable and oxygen sometimes limiting. Their occurrence in polluted areas appears to be a special case of their ability to withstand(this isn't to imply that they are individually able)highly stressed environments.

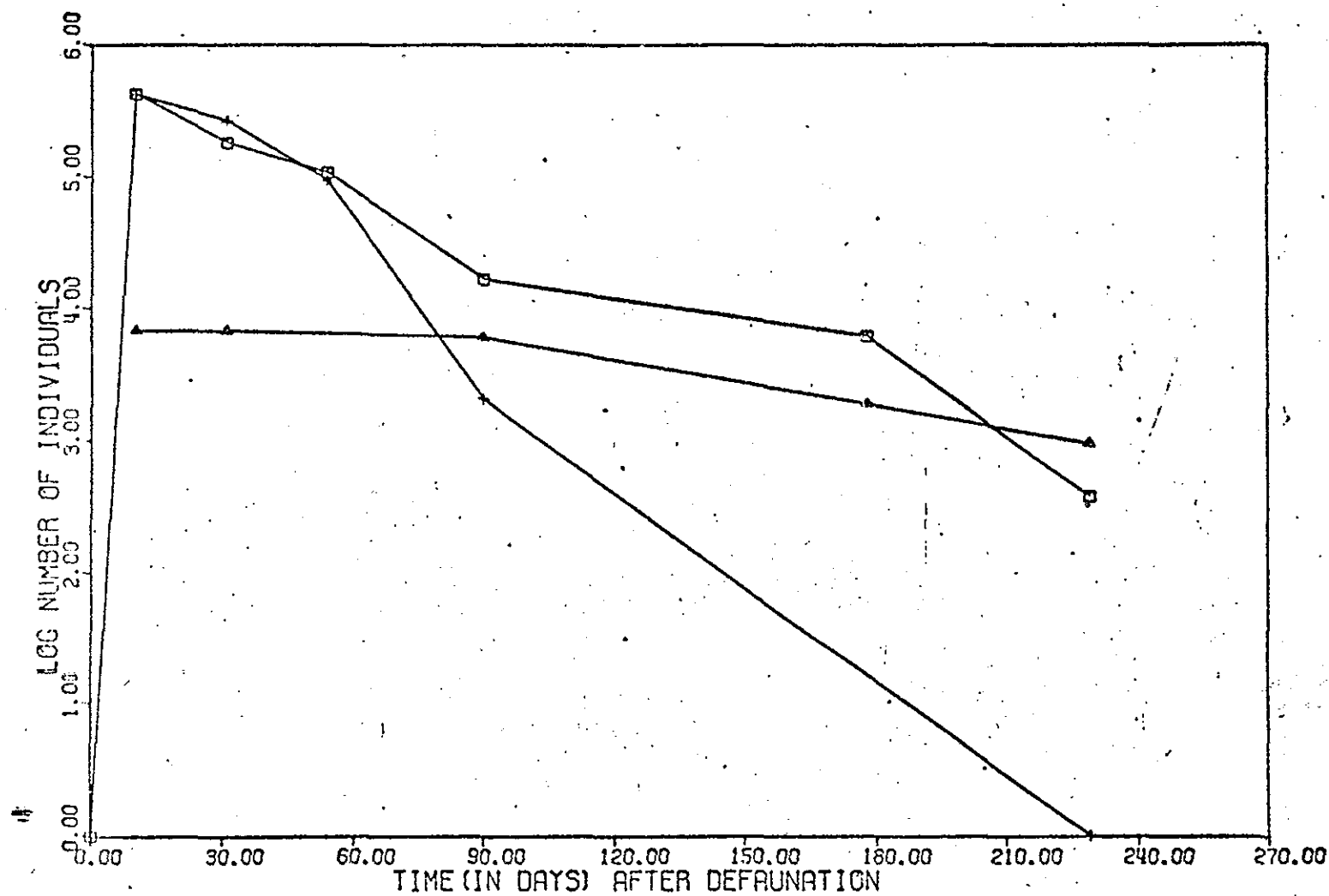
In the high densities that these two species occurred on the experimental plots, their tubes provided a stabilizing influence on the sediment in the experimental plots. Thus, the settlement of these organisms prepared the plots for future colonization by reducing erosion, reworking the sediment, and entraining sediment.

These organisms are well suited to survive in unstable situations. They are able to discover empty areas rapidly and settle in large numbers. They are poor competitors, however, and their population size is quickly reduced as more competitive species build up their population densities. (See Figures 13 & 14).

The next organism to peak, Ampelisca sp.(vadorum?) is also a tube dwelling deposit feeder(pers. comm. Alan Michaels, 1973). These small crustaceans occur in lower population densities than the initial colonizers(See Figure 15). Their tubes are also important sediment binding agents.

FIGURE 13
POPULATION DENSITY OF S. BENEDICTI OVER TIME

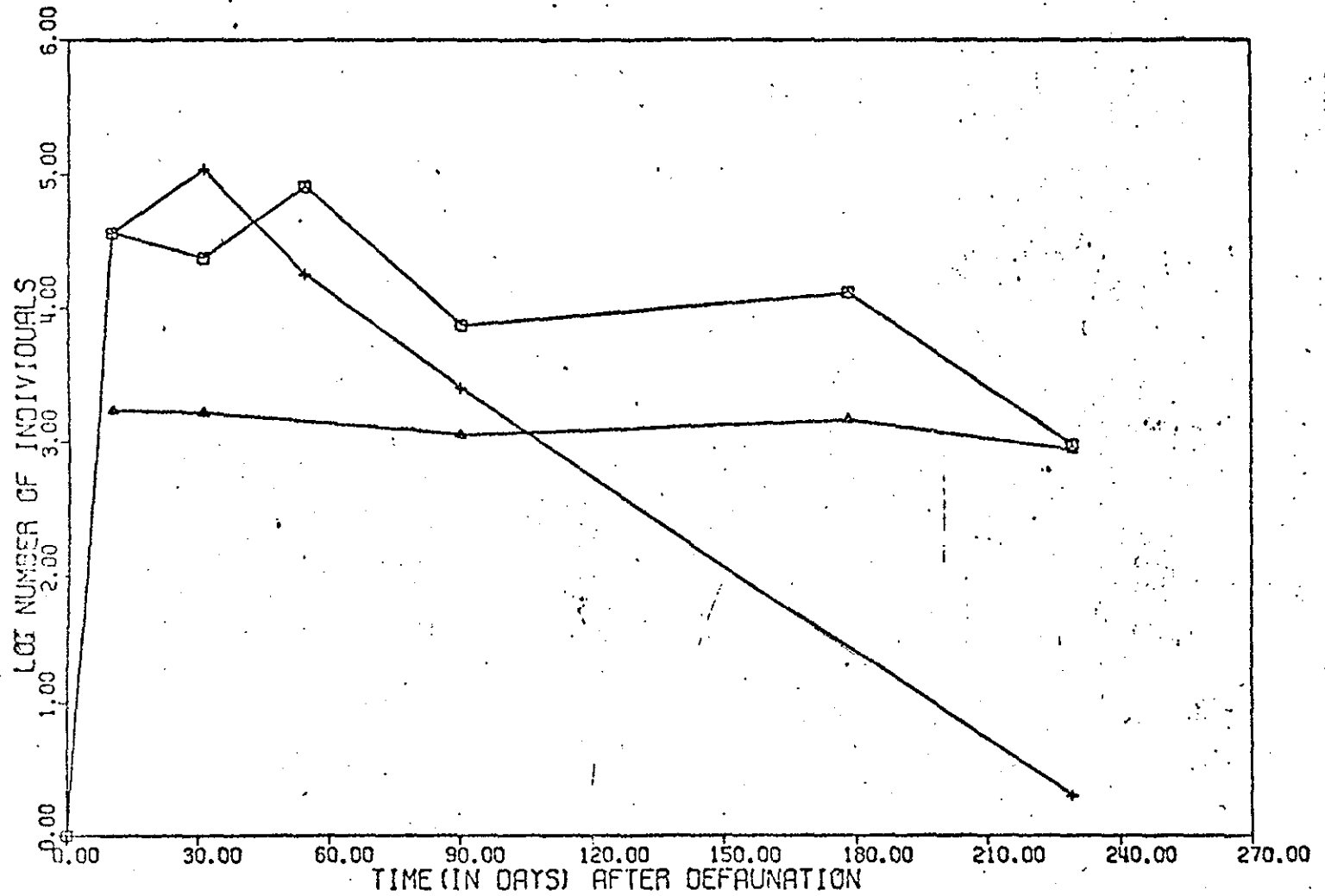
NUMBER OF STREBLOSPID AT EXPERIMENTAL SITE - 7/72-3/7



□ EXPERIMENTAL SITE - INSIDE SAMPLES
 △ EXPERIMENTAL SITE - REPLACEMENT SAMPLES
 × EXPERIMENTAL SITE - OUTSIDE SAMPLES

FIGURE 14
POPULATION DENSITY OF C. CAPITATA OVER TIME

NUMBER OF CAPITELLA AT EXP. SITE - 7/72-3/73

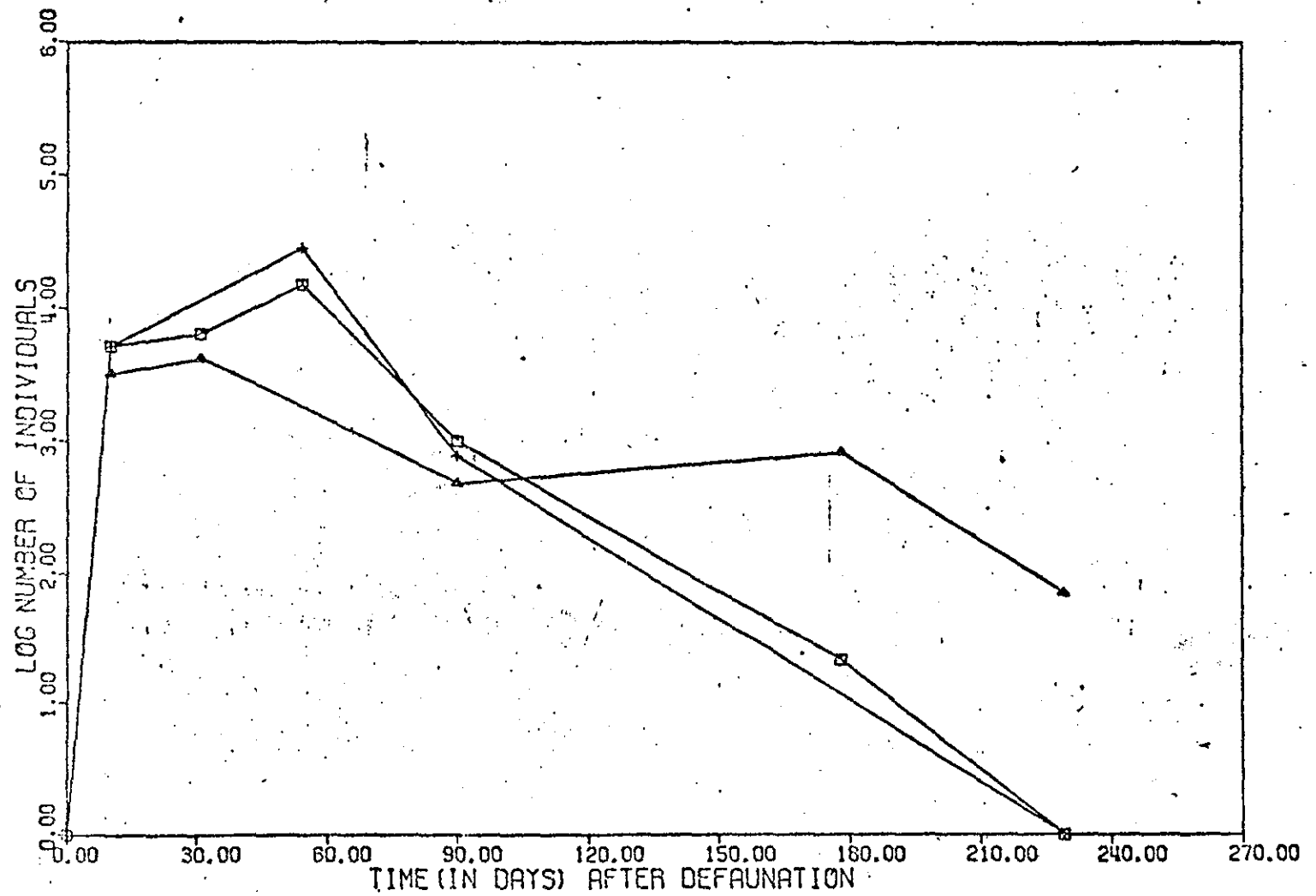


□ EXPERIMENTAL SITE - INSIDE SAMPLES
 + EXPERIMENTAL SITE - REPLACEMENT SAMPLES
 △ EXPERIMENTAL SITE - OUTSIDE SAMPLES

FIGURE 15

POPULATION DENSITY OF AMPELISCA SP. (VADORUM?) OVER TIME

NUMBER OF AMPELISCA AT EXP. SITE - 7/72-3/73



□ EXPERIMENTAL SITE - INSIDE SAMPLES
 ● EXPERIMENTAL SITE - REPLACEMENT SAMPLES
 ▲ EXPERIMENTAL SITE - OUTSIDE SAMPLES

After two months, bivalves, which up to this time had low population densities (10-200 individuals/ m²), peaked. Deposit feeders were once again the first type of bivalve to peak. (See Figures 16 & 17). Like S. benedicti and C. capitata, the two deposit feeding bivalves, Nucula proxima and Tellina agilis, utilize different parts of the deposit food resource. N. proxima, a protobranch mollusc, is a subsurface deposit feeder and is highly motile, while T. agilis feeds on surface deposit by means of two extensible siphons.

With the onset of winter all of these early peaking colonizers experience mortality. However, it must be noted here that the rate of kill off is inversely related to the order of peaking.

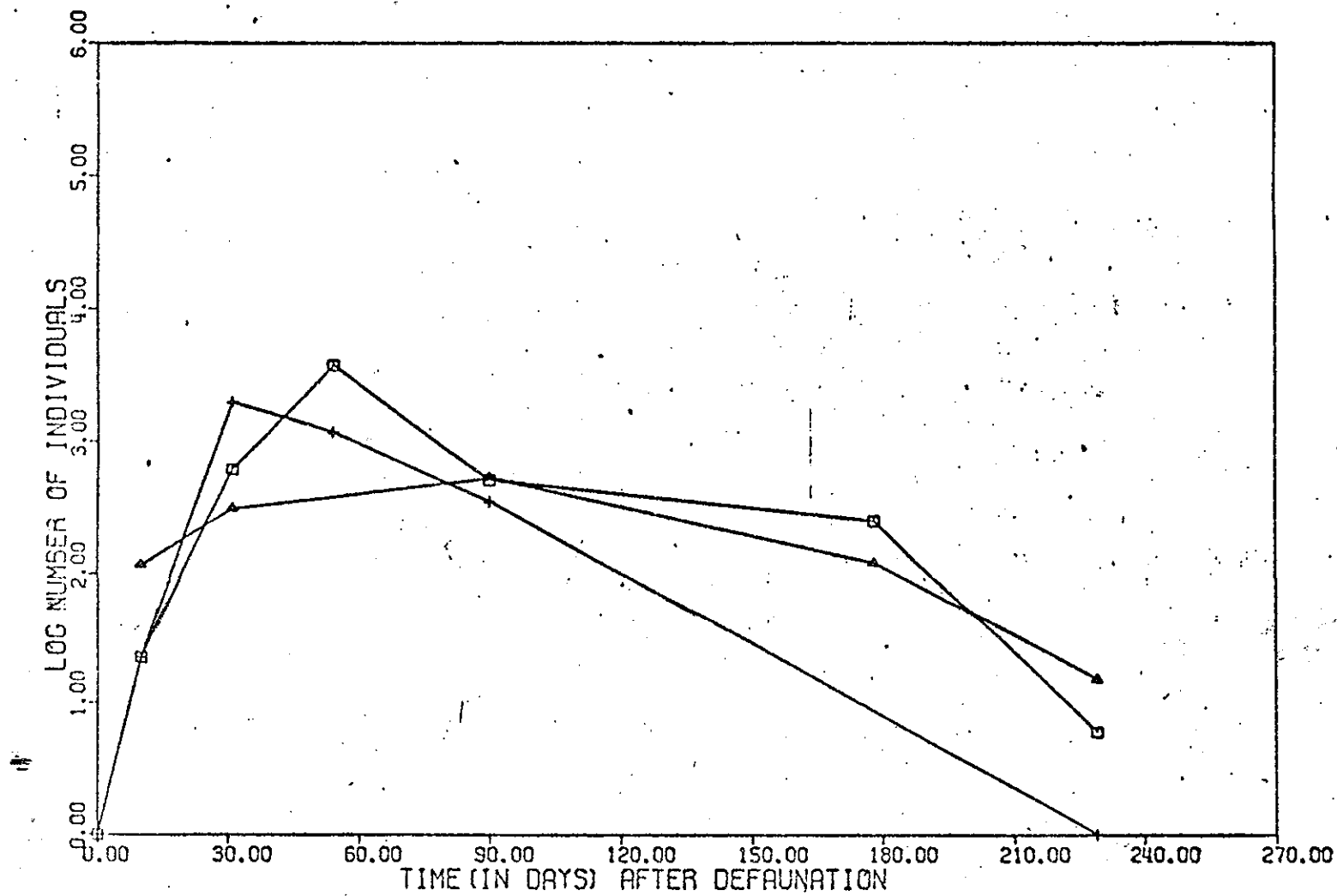
The fourth group of organisms consists of Solen viridis, a large, highly motile, filter feeding bivalve, and Neothys incisa, a large, predaceous or omnivorous, highly motile polychaete worm. These are the only species which had higher population densities outside the experimental plots than inside. (See Figures 18 & 19). These species maintained a constant population density in the face of other animals and temperature stress (N. incisa increased its population density in winter). These species are obviously poor colonizers, but they are good competitors and appear to represent the benthic "climax growth" for the experimental site.

It is seen then that the preliminary results from this study indicate that a succession or sequence does occur during recolonization of defaunated substratum. It is also clear that the two end members of this apparent succession or

FIGURE 16

POPULATION DENSITY OF NUCULA PROXIMA OVER TIME

NUMBER OF NUCULA AT EXP. SITE - 7/72-3/73

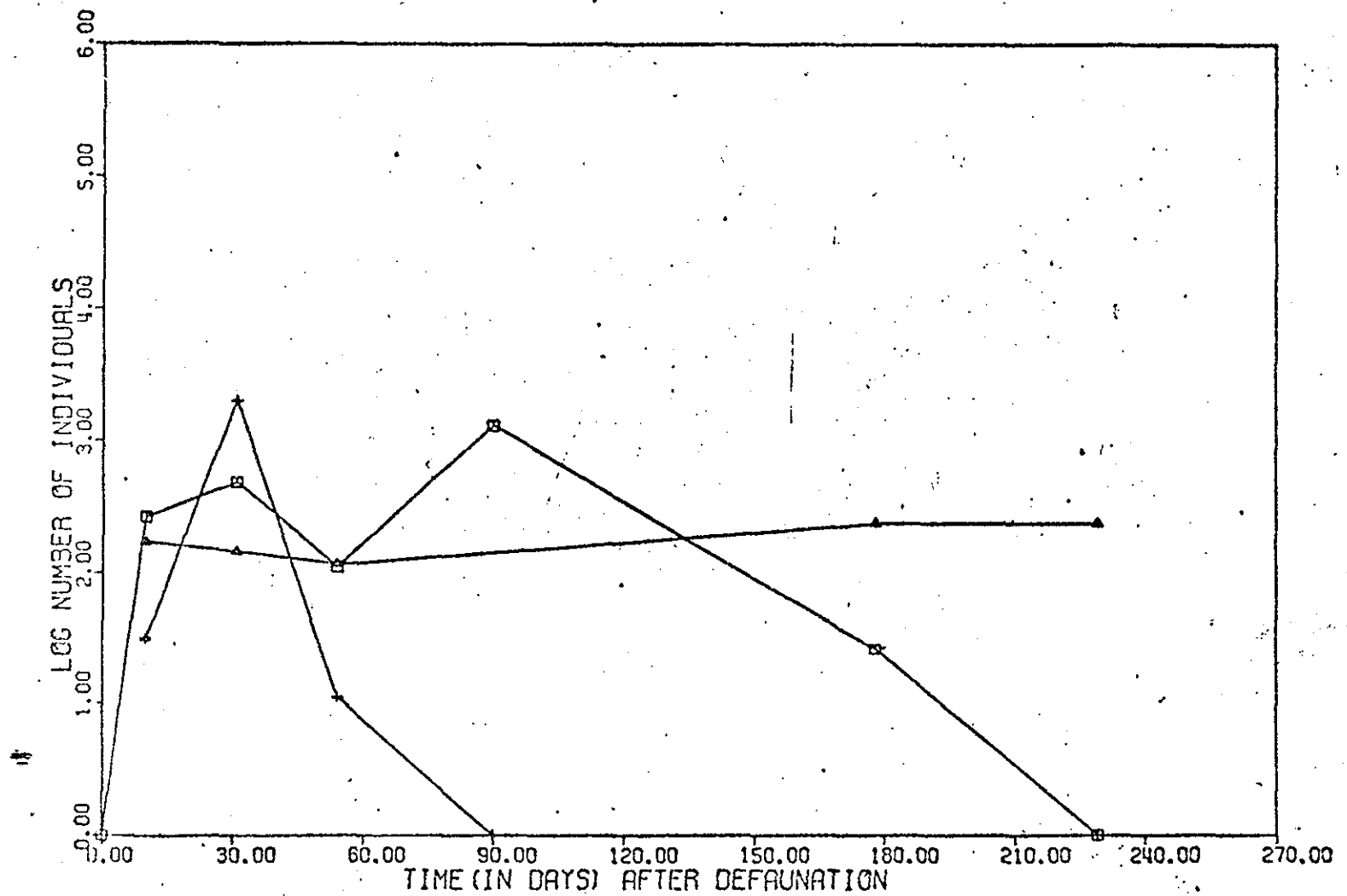


□ EXPERIMENTAL SITE - INSIDE SAMPLES
 △ EXPERIMENTAL SITE - REPLACEMENT SAMPLES
 × EXPERIMENTAL SITE - OUTSIDE SAMPLES

FIGURE 17

POPULATION DENSITY OF TELLINA AGILIS OVER TIME

NUMBER OF TELLINA AT EXP. SITE - 7/72-3/73

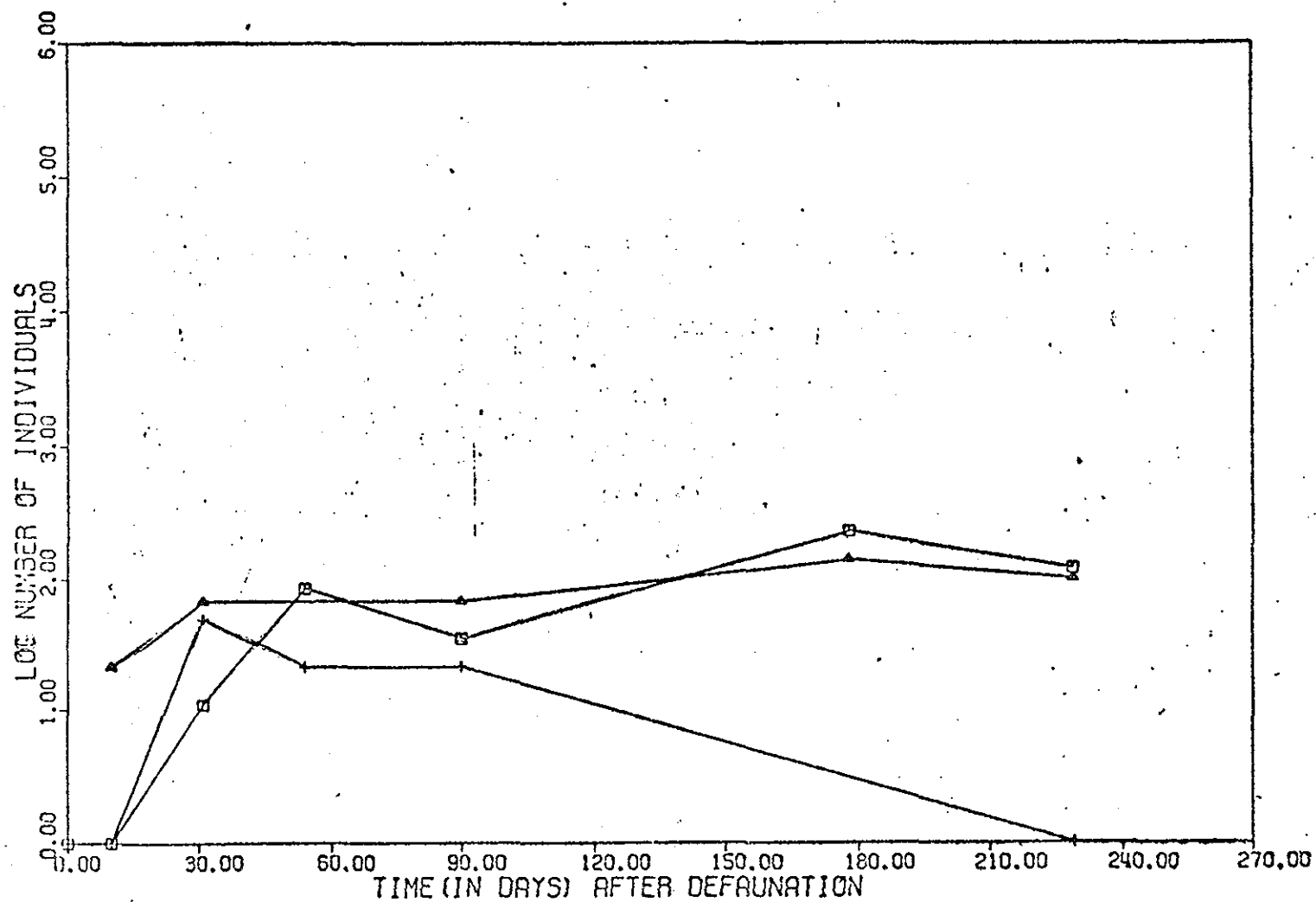


[] EXPERIMENTAL SITE - INSIDE SAMPLES
 [] EXPERIMENTAL SITE - REPLACEMENT SAMPLES
 [] EXPERIMENTAL SITE - OUTSIDE SAMPLES

FIGURE 18

POPULATION DENSITY OF NEPHTHYS INCISA OVER TIME

NUMBER OF NEPTHYS AT EXP. SITE - 7/72-3/73

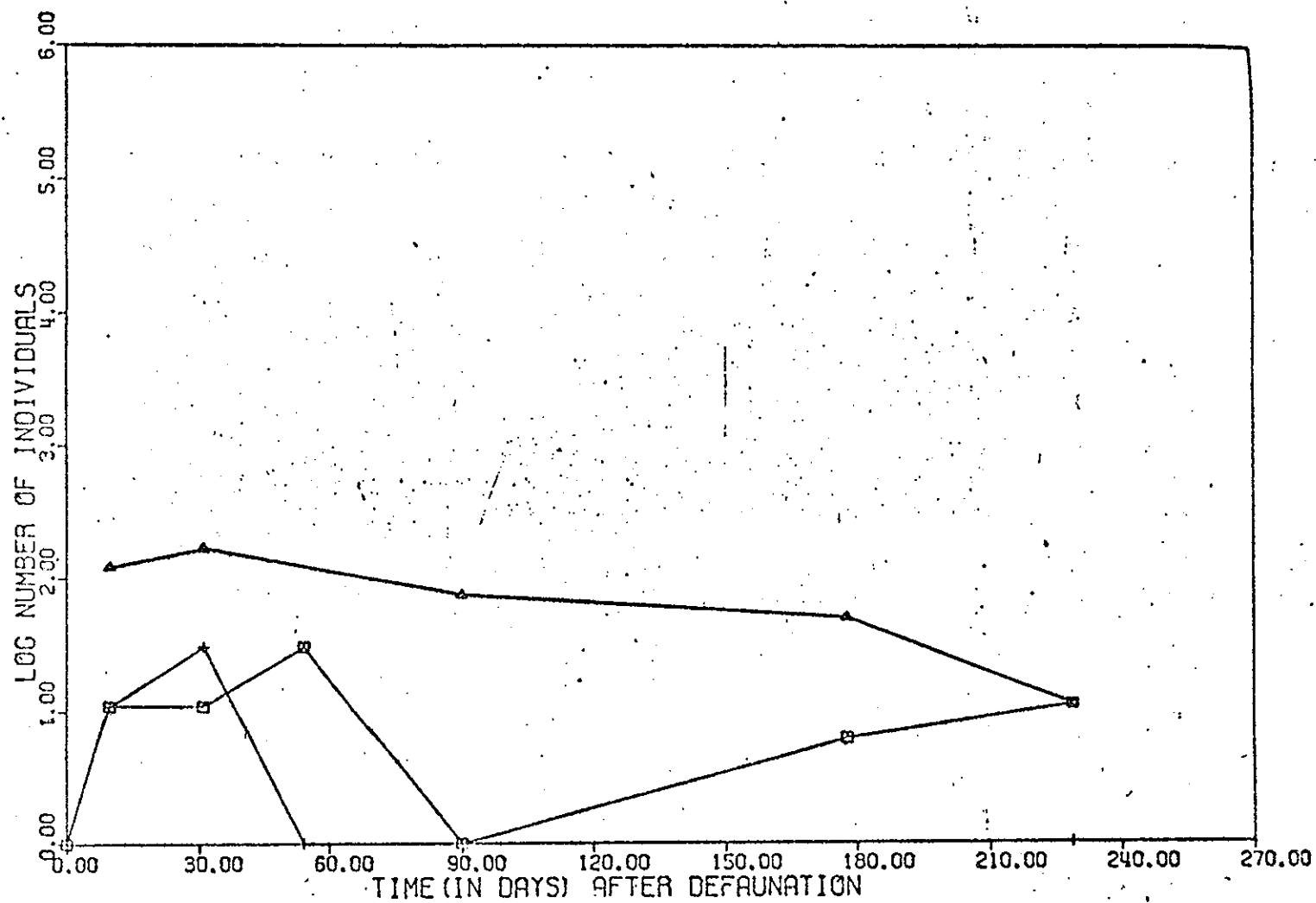


□ EXPERIMENTAL SITE - INSIDE SAMPLES
 + EXPERIMENTAL SITE - REPLACEMENT SAMPLES
 △ EXPERIMENTAL SITE - OUTSIDE SAMPLES

FIGURE 19

POPULATION DENSITY OF SOLEN VIRIDIS OVER TIME

NUMBER OF SOLEN AT EXP SITE - 7/72-3/73



□ EXPERIMENTAL SITE - INSIDE SAMPLES
 + EXPERIMENTAL SITE - REPLACEMENT SAMPLES
 △ EXPERIMENTAL SITE - OUTSIDE SAMPLES

sequence bear the following relationship:

I. Small, tube dwelling, deposit feeding organisms adapted to unstable conditions. Good colonizers, high reproductive potential, high mortality, poor competitors.

----deposit feeding bivalves---suspension feeders (small)

III. Large, mobile non-deposit feeding organisms. Poor colonizers, low reproductive potential, low mortality, good competitors.

The intermediate part of the sequence or succession is somewhat fuzzy at present, but it is hoped that studies conducted during the summer of 1973 will clear up the finer points of this process.

The sequence or succession is shown graphically in Figure 20.

IV. Additional Results

Making a quantitative estimate of the predators present at the experimental site is difficult. Diver observations indicate a large and diverse predator assemblage operating at the experimental site. These include echinoderms (Asterias forbesi), crustaceans (Libinia emarginata, Cancer spp., Homarus americanus), pices (Tautoga onitis, the tautog or blackfish, Tautoclabrus adspersus, the cunner, Raja laevis, the barn-door skate, and Pseudopleuronectes americanus, the winter flounder). These species of invertebrates and demersal fish

FIGURE 20

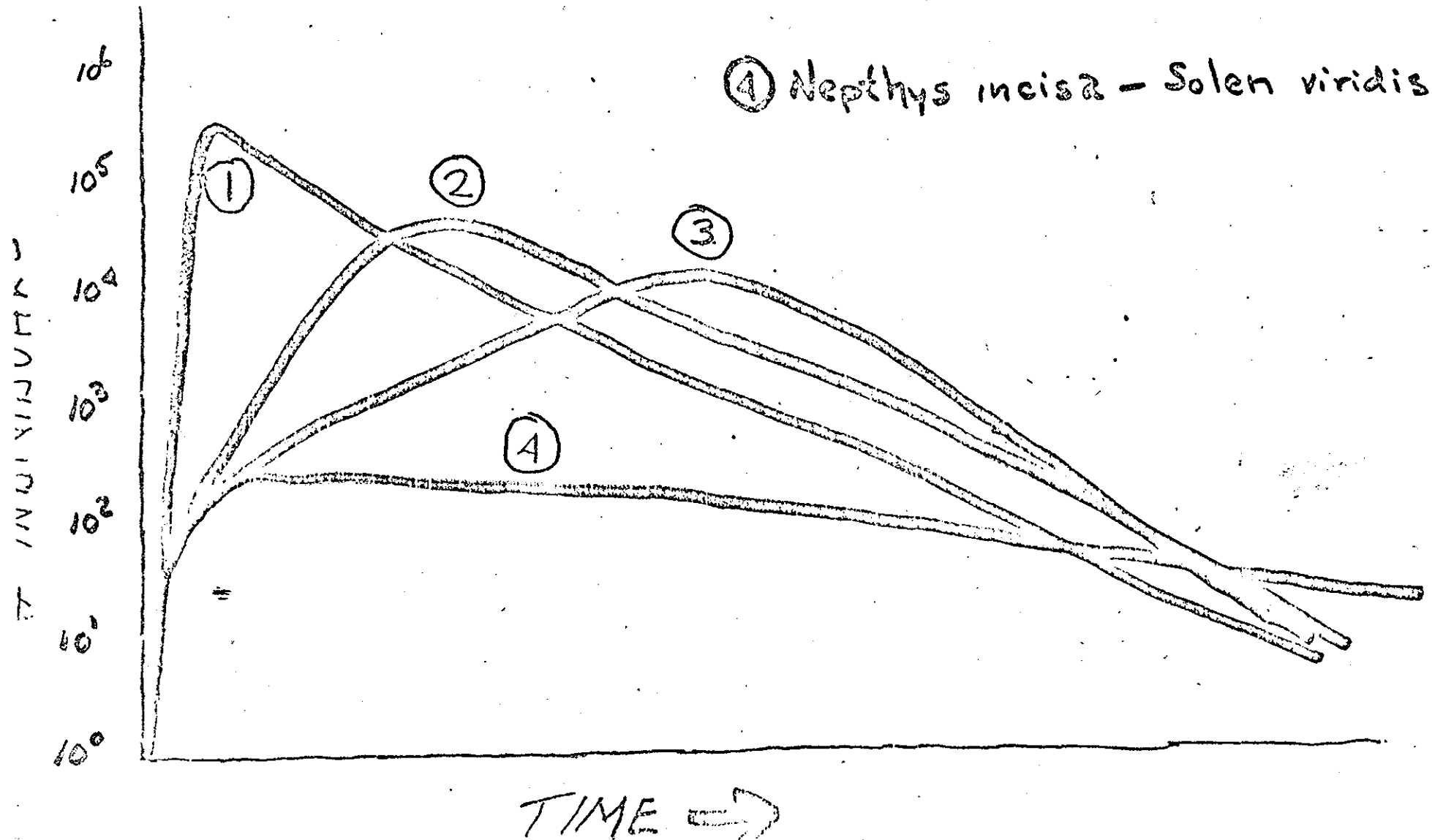
**SCHEMATIC OF SUCCESSIONAL OR SEQUENTIAL PROCESS OF
RECOLONIZATION ON EXPERIMENTAL PLOTS**

① *Streblospio benedicti* - *Caprellia capitata*

② *Ampelisca* sp. (*cradiorum*?)

③ *Nucula proxima* - *Tellina asilis*

④ *Neptysis incisa* - *Solen viridis*



are all predaceous on the small bivalves and polychaetes present at the experimental site, and should prove to be a powerful regulator of community structure and function. The experimental plots themselves are very likely a strong factor in keeping the predators (especially the crustaceans and fish) at the experimental site. Of lesser importance, at least in the number of observed occurrences are the gastropods (Busycon canaliculatum, Polinices duplicata (channeled whelk and moon snail)).

Another interesting result has been derived from the measurements of sediment water content. Water content is correlated with sediment stability, a factor of some importance to sediment dwelling organisms of both deposit and filter feeding types. The scale of sediment water content heterogeneity is quite small, varying as much as 30% over a distance of two meters. The entire scale pattern in benthic communities is liable to be much smaller than hitherto believed (see Rhoads and Young, 1971). The distribution of benthic organisms of the New Haven dredge spoil disposal area and nearby control areas as well as the benthic samples taken for the study described here also suggest this. Maps of organismal distribution over the Northwest Control site show that many organisms have extremely patchy distributions. These maps also showed that motile organisms tend to have an aggregated behavior. Many epifaunal predators exhibit this clustering behavior and it seems reasonable to assume that such clusters practice a sort of 'slain and burn' economy.

That is to say that such clusters of predators are able to defaunate areas of the bottom to a large extent, and then move on to another area. Such a practice by these motile predators would also tend to produce patchy organismal distributions.

CONCLUSIONS

The most important conclusion, tentative as it may be, is that there does appear to be a successional or at least a sequential pattern to the recolonization of defaunated substratum. Definite proof of this awaits further experimentation during the summer of 1973. If it is indeed true that a succession or sequence does exist, then it may soon be possible to determine the "health" or "grade" of a benthic community in a given environment (high latitude, with marked seasonality) with characteristic species associations simply by conventional sampling. This technique may also be extended to paleontology, since we must view patterns of organismal distribution and abundance in the benthos as the result of past events which are recorded in the present community structure. These patterns of distribution and abundance are really to be viewed as a spatial and temporal mosaic.

It appears that the infaunal benthic macrofauna of Long Island Sound is preadapted for stress placed on the

system by nature or man. There appear to be two strategies. The first strategy involves being a small, tube dwelling, deposit feeding organism with a large reproductive potential and high larval motility. The second strategy is to be a large and motile suspension feeder or omnivore with a low reproductive potential, but with good competitive characteristics. Since the benthic fauna of Long Island Sound are so adapted, any local disturbance which perturbs the existing community structure is quickly recovered from.

This conclusion has a major implication in dredge spoil dumping. If material is dumped during periods of high reproductive activity in the benthos (late spring through early fall), then the spoil material will be quickly recolonized by small tube-dwelling deposit feeders and thus stabilized. The results of the present experiment indicate that a quasi-equilibrium will be achieved on the defaunated area in approximately three months. This of course assumes that no toxic materials are present in the spoil material. If, on the other hand, the dumping of spoil material is carried out during periods of low reproductive activity (winter), the spoil material will not be quickly recolonized and bio-stabilized, but will be subject to erosion and dispersion. If the goal of the spoil dumping program is to reduce such dispersion of the dumped material, this is clearly not the time to dump dredge spoils as has been suggested by Pfitzenmeyer (1970).

It has also been argued that the dumping of the New Haven Harbor spoil material during the summer and possibly

late spring will have a deleterious effect on oyster larvae which may be killed by high turbidity levels and adult oysters in the area of the dredging which may be silted over and killed or suffocated by lack of oxygen due to high uptake of oxygen by reduced portions of the dredged sediment.

With these important considerations in mind it seems logical to dredge and dump in the early spring before the oysters begin reproducing and before the water temperature is high enough to require the oysters to be at a high metabolic level. Dredging and dumping in the early spring would also provide for spring recolonization of the spoil material before significant dispersion and erosion has taken place as would be the case in a winter deposition.

AFTERWORD

It must be stated here that the results presented in this report are preliminary in nature. Further experimentation during the summer of 1973 will be necessary to prove or disprove the successional or sequential pattern of recolonization in the benthos tentatively delineated here.

It should also be noted that the large scale grab sampling program is still incomplete. It is hoped that results from this survey will be available by the end of 1973.

REFERENCES

- Brandt, K., 1897. Das Vordringen marine Thiere indem Kaiser-Wilhelm Canal. Zool. Jahr. Abth. Syst. Geol., u. Biol. 9: 387.
- Buzas, M.A., 1965. The distribution and abundance of foraminifera in Long Island Sound: Smithsonian Misc. Coll. v.149, no. 1, 89pp.
- Gordon, R.B., K.K. Turekian, D.C. Rhoads, 1972. A report to the U.S. Army Corps of Engineers on the environmental consequences of dredge spoil disposal in central Long Island Sound: I. The New Haven spoil ground and New Haven Harbor. Manuscript.
- Gosner, K.L., 1971, Guide to Identification of Marine and Estuarine Invertebrates, Wiley, Interscience, 693 pp.
- Horn, H.S., 1971. The Adaptive Geometry of Trees. The Princeton University Press,
- Howell, B.R. and R.G.J. Skelton, 1970. The effect of china clay on bottom fauna of St. Amstell and Mewagissy Bays. Jour. Mar. Biol. U.K., 50:593
- Johnson, R.G., 1971. Animal sediment relations in shallow water benthic communities. Marine Geology, 11:93.
- MacArthur, R.H. and E.O. Wilson, 1963. An equilibrium theory of insular zoogeography. Evolution, 17:373.
- Pearce, J.B., 1970. The effects of solid waste disposal on benthic communities in the New York Bight. FAO Technical Conference on Marine Pollution and its Effects on Living Resources and Fishing, Rome 9 - 18 December 1970.
- Pfitzenmeyer, H.T., 1970. Gross physical and biological effects of overboard spoil disposal in Upper Chesapeake Bay, Project C. Benthos. Natural Resources Institute Sp. Report No. 3, Chesapeake Biological Laboratory, Solomons, Md.
- Pratt, S.D., 1972. Effects of spoil dumping on the benthic invertebrates of the Sound. in Dredge Spoil Disposal in Rhode Island Sound (Asila, S.E.:S.D.Pratt, T.T.Polgar) Marine Advisory Service, University of Rhode Island, Narragansett Bay Campus, Narragansett, Rhode Island 02882.
- Reish, D.J., 1961. A study of benthic fauna in a recently constructed boat harbor in southern California. Ecology, 42:84.

Riley, G.A., 1956. Oceanography of Long Island Sound, 1952-1954. II. Physical Oceanography. Bull. Bing. Oceanogr. Coll. 15:15.

Rhoads, D.C., 1963. Rates of sediment reworking by Yoldia limatula in Buzzards Bay, Mass., and Long Island Sound. J. Sed. Petrol. 33: 723.

----- 1967. Biogenic reworking of intertidal and subtidal sediments in Barnstable harbor and Buzzards Bay, Mass. J. Geol. 75:461.

-----, and D.K. Young, 1970. The influence of deposit feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28:150

-----, 1971. Animal-sediment relations in Cape Cod Bay, Mass. II. Reworking by Molpadia oolitica(Holothuroidea). Mar. Biol. 11:255.

Rhoads, D.C., 1973. The influence of deposit-feeding benthos on water turbidity and nutrient recycling. Am. J. Sci. 273:1.

Sanders, H.L., 1956. Oceanography of Long Island Sound, 1952-1954. X. Biology of marine bottom communities. Bull. Bing. Oceanogr. Coll. 25:345.

----- 1958. Benthic studies in Buzzards Bay. I. Animal sediment relationships. Limnol. Oceanogr. 5:245

----- 1960. Benthic studies in Buzzards Bay. II. The structure of the soft bottom community. Limnol. Oceanogr. 5:138.

-----, J.F. Grassle, G.R. Hampson, 1972. The West Falmouth oil spill. I. Biology. Woods Hole Oceanographic Institution. WHOI-72-20.

Shelford, V.E., 1935. The major communities Part I. in Some Marine Biotic Communities of the Pacific Coast of North America. Ecol. Monogr. 5:251.

Simberloff, D., 1969. Experimental zoogeography of islands III. A theory of insular colonization. Ecology. 50:296.

-----, and E.O. Wilson., 1969. Experimental zoogeography of islands. The colonization of empty islands. Ecology. 50:278.

Slobodkin, L.B. and H.L. Sanders, 1969. On the contribution of environmental predictability to species diversity. in Diversity and Stability in Ecologic Systems(Woodwell, G.H. and H.H. Smith, eds.) Brookhaven Symposium no. 22.

Smith, R.I., 1964. Key to Marine Invertebrates of the Woods Hole Region. Contribution no. 11. Systematics-Ecology Program, Marine Biological Laboratory. Woods Hole, Mass.

Stone, R.B., 1963. A quantitative study of benthic fauna in lower Chesapeake Bay with emphasis on animal-sediment relationships. M.S. Thesis, School of Marine Science, College of William and Mary.

Stone, A.N. and D.J. Reish, 1965. The effect of fresh-water run-off on a population of estuarine polychaetous annelids. Bull. Southern Calif. Acad. Sci. 64:111.

Wass, M.L., 1967. Biological and physiological basis of indicator organisms and communities. in Olson, T.A. and F.J. Burgess, Pollution and Marine Ecology, Wiley, Interscience. pp. 271-283.

Wilson, E.O. and W.H. Bossert, 1971. A Primer of Population Biology. Sinauer Associates, Inc. 192 pp.

Wilson, D.P., 1958. Some problems in larval ecology related to the localized distribution of bottom animals. in Perspective in Marine Biology. Buzzati-Traverso, A.A. (ed.) pp. 87-103. Univ. of Calif. Press. Berkeley, Calif.

Young, D.K., 1971. Effects of infauna on the sediment and seston of a subtidal environment. Vie et Milieu. suppl. 22, pp.557-571.

Dean, D., 1970. Water quality - benthic invertebrate relationships in estuaries. Ira C. Darling Center for Research, Teaching and Service, Walpole, Maine. Mimeo Report.